## *Behavioral Flexibility, Curiosity, and Cooperative Breeding: Dealing with Complex Concepts and Paradigms*

GOKCEKUS, SAMIN,YUCEL

# Behavioral Flexibility, Curiosity, and Cooperative Breeding:

*Dealing with Complex Concepts and Paradigms*

Samin Gokcekus (BA)

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Department of Psychology

Durham University

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# Contents

## Statement of Copyright

## Acknowledgments

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## General Abstract

In comparative cognition, and in empirical pursuits more generally, having clear definitions and a mutual understanding of terms and concepts is essential to producing accurate results. However, as philosophers of science Taylor & Vickers (2017) argue, many concepts today have become "fragmented" and different definitions are used in different fields on the basis of their theoretical usefulness. In an attempt not only to better understand the concept of behavioral flexibility – an organism's ability to adaptively modify behavior in response to new or changing circumstances and contingencies – but also to highlight the importance of having a coherent conceptual framework for studying any phenomena, this thesis will explore the concept of behavioral flexibility in relation to two other concepts: curiosity and cooperative breeding. I review and critically analyze the concept of behavioral flexibility in order to disambiguate the relevant cognitive processes, their behavioral manifestations, and the tasks that are used to test them. After additionally reviewing cooperative breeding and the study species, I present my novel study of curiosity and inhibition (a component of behavioral flexibility) in the cooperatively breeding common marmoset (*Callithrix jacchus*). Here, I find that group size and the interaction between breeding status, age, and curiosity score has a significant effect on inhibition score. These results provide insights in to the connections and relationships between these phenomena while also emphasizing the importance of having coherent conceptual frameworks for gaining an accurate understanding of reality, particularly in the field of comparative cognition.

# 1 - General introduction

Curiosity is a pervading and significant drive which can be understood as an internally motivated form of information seeking (Kidd & Hayden, 2015); we are constantly seeking out novel information and experiences, even when they have no obvious benefit to ourselves or our survival. Despite the fact that curiosity has been highlighted throughout history as an important factor for success in both human and non-human animals, our empirical understanding of curiosity and its functions is surprisingly undeveloped. As Loewenstein (1994) claimed in his influential review, curiosity is at the "junction of motivation and cognition," making it a vital concept to consider for understanding a myriad of pressing topics, including behavioral flexibility, personality, innovation, and cumulative culture. But what is the role that curiosity plays in the lives of humans and non-human animals. In other words, why be curious?

One route to investigating the role of curiosity is by examining it in relation to another important concept: behavioral flexibility. Behavioral flexibility can be understood as an organism's ability to adaptively modify behavior in response to new or changing circumstances and contingencies (Amici, Call, Watzek, Brosnan, & Aureli, 2018; Bonnie et al., 2012). Crucially, as Mikhalevich, Powell, & Logan (2017) point out, behavioral flexibility refers to changes not only in a behavior (as one could argue that all behavior is in response to changes in the environment), but also in terms of the rules that govern the performance of that behavior. Although behavioral flexibility is often discussed as a single mechanism or ability, it is more likely that it is an *emergent property*, arising from different mechanisms under different conditions and in different circumstances (O'Connor & Wong, 2015).

Broadly, behavioral flexibility requires the capacity to abandon old strategies and to acquire new ones. It has been suggested that behavioral flexibility is a marker of "complex cognition" and has been associated with increased fitness, intelligence, and adaptability (Amici et al., 2018; Bonnie et al., 2012; Mikhalevich et al., 2017). In terms of human evolution, Kandel et al. (2016) argue that behavioral

flexibility drove cultural innovations during the Middle Stone Age, giving it an important role in the emergence of modern human behavior. In a similar manner van Schaik et al. (2016) argue that the overwhelming feeling of curiosity played an important role in the development of human intelligence and culture through increases in exploration and innovation.

A crucial component of behavioral flexibility is the ability to abandon old strategies; one proximate control or expression of this ability is motor inhibition (Tebbich, Stereln, & Teschke, 2010). In order to try a new strategy, the prepotent motor response to perform the old strategy must be inhibited. But if curious individuals are strongly motivated to explore or approach novel and interesting stimuli, perhaps their inhibition skills are weaker; do these individuals lack the ability to inhibit random acts of exploration? On the other hand, it is possible that curiosity allows for the inhibition of fear or avoidance of novelty (Kidd & Hayden, 2015). How does inhibition, an arguably crucial component of behavioral flexibility, interact with curiosity - a drive which, theoretically, seems to be intimately related?

Behavioral flexibility can also be influenced by differences in social and reproductive systems in both humans and non-human animals. Cooperative breeding is a reproductive system where individuals other than genetic parents care for offspring (Schradin, Vuarin, & Rimbach, 2018). Because group members are working together and appear to be concerned for the same individual's survival, within-group competition is often significantly lower and social tolerance and communication higher than non-cooperative breeders (Burkart, 2009). The cooperative breeding hypothesis (CBH) posits that this type of reproductive system, and its consequences, has led to the development of unique cognitive abilities in humans (Burkart, Hrdy, & van Schaik, 2009; Burkart & van Schaik, 2016). Hrdy (2006), Kandel et al. (2016), and Damerius, Graber, Willems, & van Schaik (2017) argue that cooperative breeding, behavioral flexibility, and curiosity, respectively, enabled early humans to expand out of Africa and become the cognitively complex beings that we are today. However, to my knowledge, no studies have examined

the possible links between these concepts (cooperative breeding, behavioral flexibility, and curiosity), which themselves are not clearly defined or understood (Audet & Lefebvre, 2017; Loewenstein, 1994; Thornton et al., 2016).

## 1.1 Overview

This thesis will explore a measure of inhibition in relation to a measure of curiosity in a cooperatively breeding callitrichid species (common marmoset, *Callithrix jacchus*) in order to 1) elucidate our understanding of inhibition as a component of behavioral flexibility and how it may be related to curiosity and breeding status in cooperative breeders and 2) highlight the importance of taking other factors in to account when making conclusions about behavioral flexibility. For a number of theoretical and practical reasons, common marmosets are an excellent species to study curiosity and behavioral flexibility. For instance, they do relatively well in captivity, are cooperative breeders, and are small and relatively non-violent towards humans. First, I will take a step back and review the concept of behavioral flexibility in non-human animals and critically discuss its components as well as the measures, paradigms, and factors that are associated with it. Then, I will introduce the study species, common marmosets (*Callithrix jacchus*), and overview the relevant literature in relation to marmoset cooperative breeding. Next, I outline my novel study of inhibition and curiosity in common marmosets. My results reveal 1) a significant interaction between curiosity, age, and breeding status as well as 2) a significant effect of group size on inhibition scores, highlighting the careful deliberation that is necessary when trying to understand and explain measures of behavioral flexibility. Finally, I make suggestions for future studies of behavioral flexibility in relation to these concepts. Overall, this thesis attempts to further our understanding of some components of behavioral flexibility, curiosity, and cooperative breeding in non-

human animals and in doing so, demonstrate the importance of integrating precise definitions and holistic views of concepts for furthering our understanding.

# 2 - Behavioral flexibility in non-human animals: a comprehensive review

As individuals living in an infinitely complex and unpredictable world, humans have come incredibly far in their ability to adjust and modify their behaviors to adapt to a diverse array of environments and circumstances that are constantly changing. Innovations, ranging from agricultural and industrial practices to medical advancements, have allowed human populations to grow and survive on every continent (Bar-On, Phillips, & Milo, 2018). In other words, humans display a remarkable level of *behavioral flexibility*, which can be broadly defined as: an organism's ability to adaptively modify behavior in response to new or changing circumstances and contingencies (Audet & Lefebvre, 2017; Coppens, De Boer, & Koolhaas, 2010; Leal & Powell, 2012). A long list of non-human animals have also been reported as being capable of behavioral flexibility, but what does this (behavioral flexibility) really mean?

The concept of behavioral flexibility is used extensively in several fields, including experimental psychology, abnormal psychology, and behavioral ecology. Generally, behavioral flexibility is often understood as necessitating two components: 1) the ability to acquire new strategies and 2) the ability to abandon old strategies (Amici, Call, Watzek, Brosnan, & Aureli, 2018; Bonnie et al., 2012; Johnson-Ulrich, 2017). However, as Audet & Lefebvre (2017) point out, the concept has not been clearly defined - causing inconsistencies and conflicting results in the literature. Taylor & Vickers (2017) argue that "definitionism" – or the need to have a necessary and sufficient definition of every term – is not as widely held as it once was, which has led to "conceptual fragmentation". This view is relevant, as different notions of 'behavioral flexibility' have been used within different fields to come up with generally acceptable conclusions. Initial attempts to define and use the concept have led to the creation of a pool of several possible definitions, and it is impossible to single out a particular definition or

manifestation that is capable of accounting for all of the content of the original concept. However, different definitions are useful in different contexts; in other words, they may be evaluated based on their "theoretical usefulness."

In this way, the concept of behavioral flexibility is used very loosely and in differing contexts. In their study of reversal learning in corvids, Bond, Kamil, & Balda (2007) claim that "flexibility" can have three different meanings in the animal literature. In one sense, behavioral flexibility refers to the ability to quickly modify behaviors based on "brief, limited experience" and in reaction to "subtle variations in consequences or context" which the authors compare to the use of flexibility in an economics sense. Within the domain of engineering, behaviorally flexible individuals are "characterized as versatile, exploratory, and playful, modifying their behavior even when circumstances do not require it." Finally, behavioral flexibility can also refer to the ability to quickly reverse or change pre-potent or habitual behavior patterns; this is related to the medical connotation of flexibility.

These three senses of flexibility all influence the organism's ability to adaptively modify behavior in response to new or changing circumstances and contingencies. However, although these three connotations of behavioral flexibility may share some underlying mechanisms, the studies that look at animal behavioral flexibility are unlikely to be testing or observing the same phenomena (although there may be some overlap). By identifying components of behavioral flexibility, as well as understanding the relationships between them, we can get closer to having a comprehensive model of what behavioral flexibility is and how, why, and when individuals display it. As Griffin (2016, p. 1) argues in relation to innovation, it is likely that behavioral flexibility is "an emergent property of a larger array of traits." This "large array of traits" is what this review intends to synthesize.

Having a better understanding of the concept of behavioral flexibility in animals, its underlying mechanisms, influencing factors, and manifestation in different species is important and advantageous for five reasons.

First, understanding behavioral flexibility is important because it is crucial to our understanding of innovation, which can be broadly defined as "a new or modified learned behaviour not previously found in the population" (Reader & Laland, 2003; but see Ramsey, Bastian, & van Schaik, 2007 for alternative definitions). The human capacity to innovate has contributed to the success of our species, and this capacity has been associated with our heightened behavioral flexibility (Reader & Laland, 2003). Furthermore, as Reader, Morand-Ferron, & Flynn (2016) note, innovation is a key feature of cumulative culture: "the extensive accumulation of knowledge, and iterative improvements in technology, over time," which itself is "another defining human characteristic" (Dean, Kendal, Schapiro, Thierry, & Laland, 2012).

Second, behavioral flexibility also has been suggested to relate to the evolution of intelligence, or cognition. The ability to come up with solutions to novel problems is included in many definitions of intelligence (Reader et al., 2016). As Amici et al. (2018) note, several studies have also shown that "inter-specific differences in behavioral flexibility" are associated with "inter-specific differences in general cognitive skills," and behavioral flexibility has been understood as an integral part of intelligence (Johnson-Ulrich, 2017). Mikhalevich, Powell, & Logan (2017) defend the popular view that behavioral flexibility is evidence of cognitive complexity in animals and stress the importance of bringing together studies of ecology, evolution, and cognition to gain a better understanding of how cognitive complexity arises.

Third, behavioral flexibility is important to our understanding of human evolution more generally. After conducting an in-depth analysis of human activity in the Middle Stone Age based on measures of archeological, geographic, and ecological change, Kandel et al. (2016) conclude that behavioral flexibility itself was the main adaptation driving the adoption of cultural innovations during this time period - which is regarded by some as the corner-stone of modern human behavior (Henshilwood et al., 2002). Behavioral flexibility is thought to increase fitness via both direct and indirect

benefits, and it is thus likely favored by natural selection (Bonnie et al., 2012; Fragaszy, Visalberghi, & Robinson, 1990; Godfrey-Smith, 1996; Wright, Eberhard, Hobson, Avery, & Russello, 2010; but see Madden, Langley, Whiteside, Beardsworth, & Van Horik, 2018). Nicolakakis, Sol, & Lefebvre (2003, p. 445), who found that behavioral flexibility predicts species richness in birds argue that "behavioural innovation coupled with cultural transmission of the new skills to other members of the population could lead to greater rates of evolution. The idea is that individuals who adopt a new behaviour expose themselves to new selection pressures that may favour mutations conferring higher fitness in the new context. This should lead to the subsequent divergence of the mutants from the rest of the population and to the formation of a new species."

Fourth, in addition to being useful in studying and interpreting the abstract concepts discussed, understanding behavioral flexibility also has practical implications for animals. Every two years, the World Wide Fund for Nature (WWF) releases their Living Planet Report, which is "a comprehensive study of trends in global biodiversity and the health of the planet." In the most recent one, the foundation reports that wildlife populations have fallen by 60% over the past 50 years. As anthropogenic forces continue to destroy the natural habitats of numerous species of wildlife, the problems of rapid and unpredictable climate change and pollution are worsening and wild animals are suffering (McFarland, Barrett, Boner, Freeman, & Henzi, 2014; Rymer, Pillay, & Schradin, 2013). Understanding how animals react to change, and the extent to which they can behave flexibly in changing conditions are crucial to conservation efforts (Gruber et al., 2019; McLennan, Spagnoletti, & Hockings, 2017). Additionally, by uncovering the factors which foster or are indicative of behavioral flexibility, animals being considered for reintroduction to the wild can be assessed more thoroughly and afforded with the conditions that foster behavioral flexibility so that they will be more likely to adapt to their new environments (Vickery & Mason, 2003). Understanding behavioral flexibility can also aid in decisions of how to raise and take care of animals in zoos and sanctuaries. For example, the effects of different types

of enrichment on future behavioral flexibility can aid caretakers in their decisions about what to provide captive animals with (Wang, Marshall, & Kirkpatrick, 2017).

Finally, a detailed and comprehensive review of behavioral flexibility can help to prevent inefficiency and misunderstanding caused by conceptual fragmentation and inconsistent usage in the literature (Audet & Lefebvre, 2017; Taylor & Vickers, 2017).

To help realize these objectives and to combat the issue of conceptual fragmentation, I present a review of behavioral flexibility in non-human animals (henceforth animals). In the first section, I will discuss the concept of behavioral flexibility in relation to other, similar terms that are sometimes (erroneously) used as synonyms. In section two, I will discuss the main components of behavioral flexibility and the paradigms that are used to measure them, and critically examine the differences in these paradigms and the underlying mechanisms they may be testing. I will additionally discuss observational studies of behavioral flexibility and highlight the utility of using experimental and observational techniques together. In the third section, I will review mechanisms underlying behavioral flexibility. All in all, this review aims to inform future research on the "behavioral flexibility" of animals and contribute to making more meaningful conclusions through a comparative approach.

## 2.1 Related Terms

Given that the concept of behavioral flexibility is used very loosely and often interchangeably with other terms, it is important to understand its relationship to other similar concepts. Behavioral flexibility is often substituted with "cognitive flexibility" (Manrique & Call, 2015; Tello-Ramos, Branch, Kozlovsky, Pitera, & Pravosudov, 2019; Westbrook, Hankosky, Dwyer, & Gulley, 2018), or even "cognitive-behavioral flexibility" (Chan et al., 2002). Hurtubise & Howland (2017, p. 176) define cognitive flexibility as "an executive function that enables behavioral changes in response to new environmental

demands;" behavioral flexibility is simply the "physical manifestation" of the underlying mental processes of cognitive flexibility. While they discuss cognitive flexibility as entailing "the ability to switch between different rules or concepts" others, like Manrique & Call (2015) especially emphasize the importance of inhibiting pre-potent responses. Cognitive flexibility can be understood as what underlies behavioral flexibility.

Behavioral diversity, a term also regularly used synonymously with behavioral flexibility (Boesch, Hohmann, & Marchant, 2002), refers to variation in behavior and is similar to "motor diversity" or "the total number of unique motor patterns that a subject may exhibit" (Johnson-Ulrich, Johnson-Ulrich, & Holekamp, 2018, p. 384). Although some behaviors that are considered under the concept of behavioral diversity may be the product of behavioral flexibility, the two terms are distinct. Behavioral diversity points to variation in behavior; however, unlike behavioral flexibility, the behavior does not need to be novel, flexible, or in response to changing circumstances or contingencies.

"Flexibility" is also used interchangeably with "plasticity," (e.g. Holekamp, Swanson, & Meter's (2013). While Mathot, Wright, Kempenaers, & Dingemanse (2012) discuss behavioral plasticity in relation to methods for dealing with uncertainty, Coppens et al. (2010) discuss it in relation to a "behavioral reaction norm." Snell-Rood (2013) argues that behavioral plasticity is a type of "phenotypic plasticity" that can have two forms. Phenotypic plasticity can be defined as "the ability of an organism to alter its morphology, physiology or behavior to better match the requirements of its environment" (Lucon-Xiccato & Bisazza, 2014, p. 1) and refers to interactions between environmental influences and genetic predispositions (Foster & Sih, 2013; see Piersma & Drent, 2003 for a discussion of different 'categories' of phenotypic plasticity). Activational plasticity- "differential activation of an underlying network in different environments," can be differentiated from developmental behavioral plasticity, which refers to changes in nervous system, morphology, and physiology as a result of experience throughout development (Snell-Rood, 2013, p. 1005). These can be linked to "phenotypic flexibility" and

"developmental plasticity," respectively, which refer to the same concepts (Maille & Schradin, 2017; Rymer et al., 2013). Johnson-Ulrich (2017) speculates that behavioral flexibility is a *subset* of phenotypic plasticity. However, the concepts of "phenotypic plasticity," "behavioral plasticity," and "behavioral flexibility" have been used interchangeably in the literature, leading to inconsistencies in what is being discussed through the use of these terms, and muddling the distinctions between them (Dingemanse, Kazem, Réale, & Wright, 2010; Dingemanse & Wolf, 2013; Holekamp et al., 2013).

Mikhalevich et al. (2017) summarize the relations between these three concepts, arguing that behavioral flexibility is a "distinct type" of behavioral plasticity - as only a portion of *plastic* behaviors are flexible on the basis of experience. This rests on the idea that all behavior is plastic to some extent because it is produced in response to changing stimuli within the environment. In behavioral flexibility though, the rules that produce the behavior are altered, in addition to the behaviors themselves. So, the term behavioral flexibility should be restricted to these instances. Behavioral plasticity includes both developmental and activational plasticity (both of which may influence behavioral flexibility). Finally, behavioral plasticity is a "distinct type" of phenotypic plasticity - which itself is a more general study of how genes interact with the environment to cause changes in morphology, physiology, and life history (Mikhalevich et al., 2017; Sih, Bell, & Johnson, 2004).

As Greenberg (1990) claimed, the definition of ecological plasticity is also imprecise and unclear. He argues that there are two attributes that are discussed in relation to ecological plasticity: "lack of specialization and flexibility in the face of change" (p. 431). In their study of invasion success in birds, Sol, Timmermans, & Lefebvre (2002) argue that ecological plasticity is a correlate of niche generalism. The use of this concept is not as common,but relates to the ability to survive in different environments and conditions. The concept is discussed very broadly such as in relation to microbiota (Trosvik, Rueness, De Muinck, Moges, & Mekonnen, 2018), plants (Akinshina, Azizov, Shtonda, Khalmurzayeva, & Rakhmatullina, 2018; Čarni, Matevski, & Šilc, 2010), insects (Ayala et al., 2017; Toussaint, Hendrich,

Escalona, Porch, & Balke, 2016), birds (Díaz, 1994; N. P. P. Simon, Diamond, & Schwab, 2003) and mammals (Ménard, 2002). Although *some* demonstrations of ecological plasticity are instances of behavioral flexibility, there are important distinctions. Finally, a concept similar to behavioral flexibility is that of robustness: "the ability to succeed under a wide range of conditions" (Dukas, 2013). This is a very broad term and is not restricted to behavior. The problem here is that the 'ability' of robustness is itself influenced by many underlying abilities and factors that need to be studied and understood in order for the term to be meaningful. Again, robustness and behavioral flexibility are not synonyms.

Although the aforementioned are distinct concepts, all of them are important to the individual's ability to adapt their behavior to changes in their surroundings. These can be contrasted with the concepts of "conservatism" and "canalization." Conservatism refers to the "conservation" of behaviors, or a "reluctance to explore alternative solutions" (Harrison & Whiten, 2018). Rather than responding differently to changing surroundings, animals high in conservatism are unlikely to explore or adopt new approaches or opportunities (Brosnan & Hopper, 2014). Conservatism is related to functional fixedness - which refers to the inability of animals to come up with novel approaches to things that they have already had experience with, for example, tools (Harrison & Whiten, 2018). Similar to conservatism, canalization, refers to the "the evolutionary loss of the capacity of organisms to develop different phenotypes in different environments" (Edgell, Lynch, Trussell, & Palmer, 2009) and is essentially the opposite of phenotypic plasticity. Reviewing and differentiating these many related but distinct concepts can help us to refine research programs and the resulting literature on behavioral flexibility.

## 2.2 The components: experimental paradigms and observation

Behavioral flexibility seems to be an emergent property - something which arises as a result of several fundamental causes that cannot be reduced to them (O'Connor & Wong, 2015). As Reader & MacDonald (2003) discuss, behavioral flexibility is not tied to a unitary process or mechanism; several

underlying processes are likely to be involved. The goal of the next two sections is to identify the different routes that an individual can take to behavioral flexibility and the drivers that influence which route (if any) is taken.

### 2.2.1 Paradigms to study behavioral flexibility

The concept of behavioral flexibility is often understood as having two distinct components: 1) the ability to acquire new strategies, and 2) the ability to abandon old strategies (Amici et al., 2018; Bonnie et al., 2012; Johnson-Ulrich, 2017). These two components can be linked to two paradigms that Audet & Lefebvre (2017) discuss as popular ways to test behavioral flexibility. In comparative cognition, the ability to acquire new strategies is related to reversal-learning paradigms, which test the animal's ability to adapt their behavior to new stimulus-reward contingencies. In a typical reversal-learning task, an individual will be trained to learn an association between one stimulus and a reward. Once a "dominant response" is formed, the rule will be reversed, and the individual must learn to choose the previously unrewarded stimulus to get the reward.[1]

In their review of the neural basis of reversal learning - Izquierdo, Brigman, Radke, Rudebeck, & Holmes (2017) argue that there are three abilities implicated in reversal learning paradigms: (1) discrimination learning, (2) estimation of the likelihood that reversal will occur, and (3) a (physical) understanding of the task. However, although reversal-learning paradigms do, to some extent, test an individual's ability to acquire new strategies, there are other factors which are *not* tested through the paradigm. For example, the ability to come up with new strategies in the first place. Furthermore, the individual must abandon their old strategy during reversal-learning tasks, making it a test of this ability

[1] Generally, reversal-learning based on spatial cues is easier than reversal-learning based on visual cues (Holmes & Bitterman, 1996; Day, Ismail, & Wilczynski, 2002).

as well. Reversal learning is a specific and frequently used paradigm, but any task which requires abandoning a known association and adopting a new one requires behavioral flexibility (see Vale et al., 2017 for an example with payoff-biased learning).

Audet & Lefebvre (2017) additionally identify detour-reaching paradigms, which test "the ability to withhold or inhibit" previously deployed actions "in the face of a more immediate apparent reward" (self-control), which, in terms of behavioral flexibility, is necessary for abandoning old strategies. In these tasks, the individual must inhibit the pre-potent response of reaching directly for food that is visible to them, and instead find an alternative route around an obstruction (which is usually transparent) to get the reward. In their review of detour paradigms, Kabadayi, Bobrowicz, & Osvath (2018) argue that, although these tasks test inhibitory control, they also test several other skills, including: motor development, functional generalization, insight, and various aspects of working memory. External factors and subtle differences in task design may also influence performance on detour paradigms, for example distance to the goal, neophobia, orientation of the barrier, previous experience with transparent objects, rearing conditions, reward visibility, motivation, and age (Kabadayi, Bobrowicz, & Osvath, 2018, p. 24).

Set-shifting is another popular paradigm frequently used in studies of behavioral flexibility (reviewed in Audet & Lefebvre, 2017). Here, the individual is trained to choose between different stimuli according to a particular characteristic (e.g. shape). Similar to reversal-learning tasks, once a "dominant response" is formed, the rule is changed. Now, the individual must attend to a previously unrewarded dimension of the stimulus (e.g. color) to get the reward. Rather than learning a new association, the individual must focus its attention on the right stimulus-dimension, what Weed et al. (2008) refer to as attentional flexibility. In humans (and some primates), the Wisconsin Card Sorting Task is used to test set-shifting - where cards with different stimuli have to be matched based on varying dimensions (Heaton, Chelune, Talley, Kay, & Curtiss, 1993; Shnitko, Allen, Gonzales, Walter, & Grant, 2017; but see

Monchi, Petrides, Petre, Worsley, & Dagher, 2001). Nilsson, Alsiö, Somerville, & Clifton (2015, p. 2) argue that although set-shifting is similar to reversal learning on the surface, set-shifting is more "cognitively challenging." Unsurprisingly, many of the factors that have been identified as influencing behavioral flexibility are related to the animal's ability to direct their attention, and what they are most likely to attend to. This is because attention to relevant factors in changing environments can aid the individual not only in acquiring new strategies, but also in abandoning old ones.

Reviewing these three paradigms shows us that reversing contingencies, inhibition, and attention are all vital to behavioral flexibility. The problem here, as Audet & Lefebvre (2017) argue, is that the three paradigms, which are all used to test "behavioral flexibility", are testing skills that are made possible through different mechanisms and the use of different brain areas.[2]

The ability to acquire new strategies in natural settings (rather than in the reversal learning paradigm) rests on an individual's ability to come up with or learn new strategies, something fostered by divergent thinking (Carr, Kendal, & Flynn (2016). In human studies, divergent thinking has been defined as "the ability to generate multiple original solutions to an open-ended problem" and is associated with creativity, "the disposition of individuals to systematically pursue the generation of novel ideas, products, and procedures" (Wu et al., 2015, p. 2704; van Schaik et al., 2016, p. 1). It is often tested through the Alternative Uses Test (AUT), where participants are given an everyday object and required to come up with as many alternative ways to use it as they can (Gilhooly, Fioratou, Anthony, & Wynn, 2007). The AUT is widely accepted as a test of human creativity but is impossible to administer to animals due to verbal and representational constraints. Furthermore, as Kaufman & Kaufman (2014) argue, studies of animal creativity are often referred to as studies of problem-solving, tool-use, and

[2] There are countless studies of the underlying neural mechanisms of various measures of behavioral flexibility in humans and other animals; discussing them all is beyond the scope of this paper. For reviews see Ragozzino (2007), Floresco, Zhang, & Enomoto (2009) and Hamilton & Brigman (2015).

social learning. Consequently, there is no established method for testing divergent thinking in non-human animals.

One possible method could use the "unusual box test" developed by Hoicka, Bijvoet-Van Den Berg, Kerr, & Carberry (2013) to test divergent thinking in human toddlers, where individuals are presented with a box with novel items and multiple compartments and parts that can be manipulated. These are similar to "curiosity boxes" (Banta, 1970), which were used to test children's curiosity and behavior towards novelty in the late 1900's. Variables include the individual's latency to approach and the number of different ways they manipulate the box. In their study of innovative problem solving in wild hyenas *(Crocuta crocuta*) Benson-Amram & Holekamp (2012) emphasize the importance of "the diversity of initial exploratory behaviors" for problem-solving success. Divergent thinking and curiosity are related to similar factors like neophilia, motivation, and exploratory behavior (discussed later) and may have common underlying factors.

Perhaps the most similar example used in animal studies is the "multi-access box" paradigm (Huebner & Fichtel, 2015; Johnson-Ulrich et al., 2018). Although box design can vary widely across studies, there is always a box with a baited food compartment in the center that can be accessed using multiple strategies or sequences of actions. Often times, the number of different manipulations and strategies observed is used to evaluate the individual's propensity for innovation. Multi-access boxes are more complex versions of what are called "extractive foraging tasks" (also known as 'artificial fruits' - Whiten, Custance, Gomez, Teixidor, & Bard, 1996) which test the animal's ability to obtain food that is not immediately accessible from an artificial or natural substrate (Day, Coe, Kendal, & Laland, 2003). The multi-access box and extractive foraging tasks additionally test persistence, motor diversity, and some aspects of cognition (Audet & Lefebvre, 2017).

However, there is a big difference between the boxes used with human children and the tasks given to animals. In the multi-access box and extractive foraging tasks there is always a food reward that

the animal is trying to retrieve, whereas children are presented with boxes (not rewards) to explore freely and according to their own interest. This can have an effect on the results obtained (but see Carr, Kendal, & Flynn, 2015; Wood, Kendal, & Flynn, 2015 for examples with stickers). In a recent study by Ebel & Call (2018), great apes whose first experience of the test apparatus was when it was unbaited were quicker to solve the task than great apes who had the opposite order of introduction. Additionally, the presence of food can lead to different effects for different individuals. If an individual is not motivated to retrieve the food, they will probably give up after a few trials. On the other hand, if the individual is extremely motivated to retrieve the food, they may become so focused on the food reward that they are unable to attend to other important features of the problem which may prevent them from successfully solving the task (Ebel & Call, 2018). Multi-access boxes and extractive foraging tasks can be considered problem-solving tasks - and are more closely associated with physical cognition, motor skills, persistence, and inhibition. On the other hand, unusual and curiosity boxes depend on the individual's own motivation to approach and interact with novelty - and are more closely associated with various internal and external characteristics like neophilia, motivation, exploratory behavior, play, and the novelty, complexity, and safety afforded by the environment; further studies with unusual and curiosity boxes can help us to better understand these characteristics.

Some studies measure behavioral flexibility through paradigms that entail *both* the ability to acquire new strategies and to abandon old ones. The details of these tasks can be very different, but they all have a similar set up (I will refer to them as strategy prevention paradigms). First, the individual is presented with a foraging task where they must either find or learn a strategy to retrieve a reward. Once the individuals show a consistent use of that particular strategy, the strategy is either blocked or made inefficient, and the individual must find an alternative strategy to retrieve the reward (Bonnie et al., 2012; Harrison & Whiten, 2018; Hrubesch, Preuschoft, & van Schaik, 2009; Huebner & Fichtel, 2015).

Token exchange paradigms, which have exclusively been used to study primates, are also discussed as a measure of behavioral flexibility and have yielded mixed results (Hopper, Kurtycz, Ross, & Bonnie, 2015; van Leeuwen, Cronin, Schütte, Call, & Haun, 2013). In these studies, individuals (usually chimpanzees) are given a non-food item, "tokens," that can be exchanged for a low- or high- value food item (based on preference) over time and in different locations. Individuals are usually trained using a single token or location, and their subsequent use of the token is monitored to look at how their behavior differs from the initial models' and if their behavior changes when the reward that each token yields is manipulated over time or with changing locations (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Vale et al., 2017). This paradigm can also be modified to act as a test of self-control or planning for the future, by giving individuals the option to choose between a low-value food item or a token that can be exchanged for a high-value food item later on (Beran & Evans, 2012; Bourjade, Call, Pelé, Maumy, & Dufour, 2014; Judge & Essler, 2013). Like the others, this paradigm is testing a myriad of skills, for example, observational learning, and can be influenced by other factors like status and competition; consequently caution is required when interpreting these results as markers of behavioral flexibility (Addessi, Mancini, Crescimbene, & Visalberghi, 2011; Bevacqua et al., 2013).

Finally, it is important to note other limitations that come with experimental studies. For example, van Horik & Madden (2016) discuss the possibility that the results of experimental tasks are biased because of *who* is more likely to participate in them. They report that sex, body condition, personality traits, and habituation to testing procedures can influence which individuals will participate in cognitive tasks. This can cause sampling biases that make it harder to study the full range of individual differences in various measures. In their study of memory tests with New World monkeys, Schubiger, Kissling, & Burkart (2016) discuss the motivational biases that influence performance in tasks involving memory. They claim that tasks with two choices may not produce accurate results in terms of physical cognition; as the number of choices increases, the probability that a random guess will result in

reward becomes lower. Because of this, individuals seem to perform better on tasks with a higher number of choices. Thus, variation in experimental measures commonly used to test behavioral flexibility may influence results and cause differences among studies that are not necessarily associated with differences between the subjects being studied.

### 2.2.2 Observational methods to study behavioral flexibility

Observational studies of behavioral flexibility in the wild tend to take a somewhat different approach (Huebner & Fichtel, 2015). Rather than using tasks to assess abilities or cognitive processes that are believed to underlie behavioral flexibility, these studies will instead observe behaviors that are thought to be manifestations of behavioral flexibility. Theoretically, the paradigms discussed in the previous section *should* underlie the flexibility in behavior that is identified in observational studies. I will review various observational studies of behavioral flexibility in the wild related to innovation, feeding ecology, social learning, play, and communication signals and displays.

#### *2.2.2.1 Innovation*

Many have argued that instances of innovation are a manifestation of behavioral flexibility (Biondi, Bó, & Vassallo, 2010; Overington, Morand-Ferron, Boogert, & Lefebvre, 2009). Reader et al. (2016) claim that innovation rates can be used as estimates of behavioral flexibility - as innovative species are more likely to adapt to new environments. In an influential study, Sol & Lefebvre (2000) looked at the invasion success of 39 avian species that had been introduced in New Zealand in relation to their relative brain size and foraging innovation rates. In addition to those with larger brains, species who had successfully invaded their new habitats displayed significantly higher rates of foraging innovations in their previous location. In other words, innovative taxa were more successful in adapting to new environments.  Behavioral flexibility may also be measured by looking at 'innovative' behavior.

For example, Knaebe, Taylor, Elliffe, & Gray (2017) discuss the flexibility of new Caledonian crows in their tool-making efforts – who alter the length of the tools they are given according to changing circumstances in an attempt to gain a food reward.

Reader & MacDonald (2003) claim that innovation alone can be a reliable indicator of species differences in behavioral flexibility. However, it is erroneous to equate the two concepts, as some factors that have a positive influence on the propensity for innovation simultaneously prevent behavioral flexibility (Audet & Lefebvre, 2017). For example, while persistence has been considered important for the production of innovations, it is also understood as the opposite of flexibility (Hommel, 2015; Huebner & Fichtel, 2015). Furthermore, species that are described as having high behavioral flexibility are not always successful in problem solving tasks that purport to test innovativeness (Logan, 2016a, 2016b). Many of the factors that influence behavioral flexibility (discussed in the following section) are also relevant to innovation, but the two concepts are not the same. Therefore, behavioral flexibility cannot be measured through the use of innovation rates on their own.

#### *2.2.2.2 Feeding ecology*

One of the most common manifestations of behavioral flexibility can be seen in animal foraging tactics and strategies, whereby individuals adjust their food preferences to adapt to changing environments (Jones, 2005).[3] For example, Herborn, Heidinger, Alexander, & Arnold (2014) observed the foraging behavior of wild blue tits (*Cyanistes caeruleus*) on an artificial` feeder. Individuals were subsequently captured and tested for their exploratory tendencies and neophobia. Behavioral flexibility was measured by observing the tendency of individuals to adjust their use of the artificial feeder depending on the air temperature throughout the winter. They found that high neophobia, high

[3] Unsurprisingly, dietary changes are the most common adjustment made in reaction to the negative effects caused by anthropogenic forces (McLennan et al., 2017). This is followed by social adjustments and responses to novelty.

exploratory behavior, and older age was associated with (flexible) temperature-dependent feeder use. In another avian study, Harding et al. (2007) looked at the relationship between prey density and the foraging behavior of common mures (*Uria aalge*) were able to differentially adjust the amount of time they spent on foraging in periods of low, medium, and high food availability. The authors speculate that this flexibility may be related to the fact that mures have "patchy and ephemeral" food sources. The idea that high variability in resources fosters behavioral flexibility will be discussed further in the section on contextual factors.

Similarly, Lloyd, (2017) found that sanje mangabeys (*Cercocebus sanjei*) adjusted their foraging behavior and the locations they selected (ranging) in response to both high and low food availability in terms of the type of resources available and the density of those resources. She argues that this behavioral flexibility may be related to the "exceptionally diverse ecological conditions" that her study group has been exposed to, as well as the wide range of foods that they consume (p. 100). Parrots (*Forpus canthopterygius*) adjust their foraging behavior in relation to the availability of fleshy fruit (Silva & Melo, 2018); this may be related to factors similar to those discussed by Lloyd (2017). Animals can also alter their foraging behavior in relation to climate (Green, Boyd, Woakes, Warren, & Butler, 2005). Similar to the birds in Herborn et al.'s (2014) study, vervet monkeys (*Chlorocebus pygerythrus*) differentially adjust the proportion of the time they spend feeding in relation to high and low temperatures (McFarland et al., 2014).

#### *2.2.2.3 Social learning*

While learning, by definition, is always necessary for behavioral flexibility (Dukas, 2013), the role of social learning is not as clear. Reader & Laland (2003) find that social learning is associated with innovation in primates, while others argue that it promotes conformity and suppresses innovation. Galef (2003) discusses these contrasting views. On the basis of his numerous experiments with both wild and

domesticated rats, Galef (2003, p. 140) claims that social learning promotes neither conformity nor novelty; the role it plays is dependent on "an animal's behavioural proclivities and individual experiences."

Burkart, Strasser, & Foglia (2009) found that social learning in common marmosets (*Callithrix jacchus*) was negatively correlated with what they refer to as type 2 innovation - "the propensity to realize and switch to a novel, but easier solution after the establishment of a well-learned solution" but not with type 1 innovation - the ability to generate novel solutions to old or novel problems. Day et al. (2003) found that social learning (measured through social attentiveness) was correlated with more successful (and unsuccessful) responses to an extractive-foraging task and shorter latencies to approach the tasks in other callitrichid species. But this effect is not unique to primates - after exposing trained bumblebees to various demonstrators that moved a ball to a particular location to retrieve a reward, Loukola, Perry, Coscos, & Chittka (2017) found that individuals were able to generalize the behaviors of the demonstrators to the specific situation that they were in (changes in location and color), and most (25 of 30) did this successfully on their first try. The authors argue that the bees are able to solve the task not only by relying on the demonstrator but also improving the original strategy by generalizing the demonstrator's behavior to their own situation - a display of "an unprecedented degree of behavioral flexibility" (Loukola et al., 2017, p. 833). The effect of social learning on behavioral flexibility remains unclear (Aplin, Sheldon, & McElreath, 2017).

Changes in social behavior have also been used to study behavioral flexibility. In Lloyd's (2017) study, sanje mangabeys adjusted their physical positions within the social group in order to prevent possible feeding competition. Rymer et al. (2013) discuss the "social flexibility" of mice (*Rhabdomys pumilio*) in relation to their ability to switch breeding tactics (solitary vs. communal) in relation to population density and available resources. In the social domain, studies of tactical deception - "when an individual is able to use an 'honest' act from his normal repertoire in a different context to mislead

familiar individuals" (Whiten & Byrne, 1988, p. 233) - have been linked to the concept of behavioral flexibility (Montgomery, 2014). For example, ravens (*Corvus corax*) adjust their behavior depending on the social context; individuals who steal food from caches will refrain from doing so *if* the individual who constructed the cache is present (Bugnyar & Heinrich, 2006). A slightly looser definition of deception can include the withholding of information. For example, primates may not emit food calls upon locating food so that they can eat it themselves (Brosnan & DeWaal, 2001) – which is also related to inhibition.

#### *2.2.2.4 Play*

Play has also been described as a demonstration of behavioral flexibility because it leads to the generation of novel behaviors. As discussed by Fagen (1982), it has long been hypothesized that play in infancy and youth enhances behavioral flexibility in adulthood by affording the individual with the experience necessary to develop complex skills in the social and physical domain, enabling the adoption of new strategies in the face of changing conditions. Furthermore, it is possible that by exploring objects through play, individuals understand how objects enhance or change the actions and motions that they are capable of and can subsequently tune their motor behaviors and understanding of physical causation (Kahrs & Lockman, 2014). Play in social settings can also facilitate an understanding of social relationships and assessments of abilities and competitive skills (Yanagi & Berman, 2017). Palagi (2006) argues that frequent and rough social play in early life affords female bonobos (*Pan paniscus*) the enhanced behavioral flexibility and social competence necessary for their peaceful and egalitarian lifestyle. Because play behaviors are flexible, rather than reflexive reactions to the environment, play and behavioral flexibility seem to have a reciprocal relationship (Kuczaj II & Horback, 2012).

Using datasets from several studies relating behavioral flexibility, brain growth, life history traits, and play behavior in primates, Montgomery (2014) tested the hypothesis that play functions to foster the development of cognitive complexity and behavioral flexibility. He reports a strong positive

relationship between play activity and postnatal brain growth - suggesting that play allows for the refinement of motor controls and adult behaviors during a period while the brain is developing and becoming myelinated. Additionally, Montgomery (2014) discusses the association between play and flexible behaviors, noting that social play was related to the generation of social behaviors (tactical deception), while non-social play was related to non-social behaviors (tool-use, innovation, extractive foraging). It seems that play has an intimate and perhaps reciprocal relationship with behavioral flexibility, especially during early life.

#### *2.2.2.5 Communication signals and displays*

Finally, the use of communicative signals and displays have also been characterized as indicators of behavioral flexibility. Although it was not designed to test behavioral flexibility, Lameira & Call's (2018) recent study on alarm calls in sumatran orangutans (*Pongo abelii*) represents an example of how animals can exhibit flexibility in this domain. Orangutan mothers were exposed to tiger-like animal models for 2 minutes in order to look at their alarm call responses, which are usually elicited by orangutans in response to predators. The results showed that orangutan mothers delayed their alarm call for up to 17 minutes after being presented to the predator or did not respond with a call. Furthermore, orangutan mothers whose infants were younger were more likely to alarm call. Presumably, orangutan mothers delay their alarm calls (or do not alarm call) in order to prevent detection and protect their young from danger. These results seem to show a manifestation of behavioral flexibility. Although orangutan's usually respond to predators with alarm calls, the orangutan mothers *inhibited* the alarm call response in order to keep their infant safe. However, mothers with younger infants still responded with the alarm call (even if it was delayed), which the authors argue is initiated so that the infant will learn that encounters with predators are dangerous. By delaying the call,

the orangutan mother is able to keep herself and her infant safe while also providing her infant with crucial information about the presence of predators.

Other factors observed in relation to behavioral flexibility include: reactions to predators (Couchoux & Cresswell, 2012; Kern & Radford, 2014; Stökl, Machacek, & Ruther, 2015), mating and sexual behavior (Bardier, Aisenberg, Toscano-Gadea, & Costa, 2015; Dunbar & Shultz, 2007; Peretti & Carrera, 2005; Rossmanith, Grimm, Blaum, & Jeltsch, 2006), and migration and patterns of habitat use - sometimes measuring responses to anthropogenic forces and change (Barbaresi, Santini, Tricarico, & Gherardi, 2004; Blumroeder, Eccard, & Blaum, 2012; Lowry, Lill, & Wong, 2013; Mekonnen et al., 2018; Sol, Lapiedra, & González-Lagos, 2013; Zuberogoitia et al., 2010).

### 2.2.3 Using experimentation and observation simultaneously

How do observations of behavioral flexibility in more natural environments relate to performance on experimental paradigms? Lehner, Burkart, & van Schaik (2011) used a strategy prevention paradigm with seven captive orangutans (*Pongo pygmaeus abelii*). Individuals were presented with a transparent tube filled ¼ of the way with maple syrup; they were also given sticks, leafy twigs, wood wool, and paper. In the next stage, the tube diameter was decreased, making some of the previously used strategies inefficient. In the final stage, the leafy twigs were removed - so that individuals would no longer be able to use the strategy that is used most often in the wild (branch scoop). Throughout the study, individuals continued to search for new strategies, even when their own solution was efficient. When the tube was made smaller, individuals tried new strategies that were "functional and efficient" but had not been employed before. When the leafy twigs were removed, individuals again adjusted their strategies. The authors argue that orangutans demonstrate a high degree of behavioral flexibility.

Orangutans have also been found to be the most successful in inhibitory control out of all the great ape species as well as behavioural flexibility Amici et al. (2018). For instance, in a detour reaching task, orangutans (*Pongo pygmaeus*) outperformed gorillas (*Gorilla gorilla*), bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*) and human children (Vlamings, Hare, & Call, 2010). Orangutans have also been described as culturally innovative (Russon et al., 2009; van Schaik et al., 2003).

While experimental measures of behavioral flexibility are testing the *propensity* for behavioral flexibility and the factors which may influence it, observational measures in the wild are a measure of the group's *current* behavioral flexibility. Both types are important. Through the use of both observational and experimental studies and the testing of clearly defined *components* of behavioral flexibility, it is possible to come up with more detailed models.

Thus far, reviewing the literature on behavioral flexibility makes it clear that behavioral flexibility is not a unitary concept that can be studied directly. Instead the underlying components and the ways they interact with one another can be assessed to gain a holistic view of behavioral flexibility. As Sol et al. (2002) argue, the components of behavioral flexibility may be uncorrelated or their effects may be context dependent - requiring a more thorough and holistic understanding of the components of behavioral flexibility. In the next section, I will provide a detailed summary of the factors and characteristics (individual, cognitive, personality, contextual, species) that influence behavioral flexibility and discuss interactions between them.

## 2.3 Mechanisms of behavioral flexibility

### 2.3.1 Cognitive Processes

If cognitive flexibility is the physical basis of behavioral flexibility, then cognitive processes, by definition, are crucial to behavioral flexibility (Hurtubise & Howland, 2017). The ability to generate

flexible behaviors is often associated with cognition - despite the fact that cognition is not defined in terms of behavior (Mikhalevich et al., 2017). With these considerations in mind, it is easy to see that cognitive processes are crucial to behavioral flexibility. Below, some cognitive processes are discussed.

#### *2.3.1.1 Attention*

As discussed, attention plays a crucial role in behavioral flexibility. In the context of behavioral flexibility, attention can be understood as a "determinant of perception," which includes "processes ensuring appropriate and continued maintenance and selection of stimuli for goal-directed behavior" (Nilsson et al., 2015, p. 4). The importance of attention in behavioral flexibility is emphasized by the negative influence of proactive interference (Croston et al., 2017; Tello-Ramos et al., 2019), which refers to previously learned information that interferes with the learning and/or retention of new information (see Baker, Raynor, Francis, & Mizumori, 2017 for a discussion).

If an individual pays more attention to a novel object or piece of information, they are more likely to encode it, and consequently remember it (Chun & Turk-Browne, 2007). Therefore, it seems that, if you remember novels things better, you might be more likely to act upon them; the weight of the new information can outweigh the weight of the prior information - preventing proactive interference. Kang et al. (2009) found that high levels of curiosity about novel information in humans enhanced the later recall. They suggest that curiosity helps to consolidate memory of novel information. In a study examining the induction and relief of perceptual curiosity through the visual representation of objects, Jepma, Verdonschot, van Steenbergen, Rombouts, & Nieuwenhuis (2012) found that perceptual curiosity was associated with increased neural activity in the striatum and hippocampus, correlating with enhanced reward circuitry, motivation, and recall ability. So, what the individual attends to (especially in novel situations) is crucial to their propensity for behavioral flexibility. Attention toward

conspecifics may also influence behavioral flexibility through low-fidelity social learning (Day et al., 2003).

This discussion can also be related to the concept of appraisal - where the individual combines information about internal "affective states" and "momentary environmental conditions," in order to detect and assess the importance of an event or stimulus and whether or not they should engage with it further (Faustino, Oliveira, & Oliveira, 2015, p. 2). In other words, appraisals help the animal to direct their attention and sustain it in situations that are evaluated as important or relevant. Faustino and colleagues (2015) discuss "appraisal components," characteristics like novelty, predictability, and pleasantness as well as cognitive biases, which aid the animal in the appraisal process. So, attention and appraisal - both of which are crucial to behavioral flexibility - may be moderated through responses to novelty and personality factors like curiosity, but also by contextual factors and the characteristics of the individuals' species (discussed later).

#### *2.3.1.2 Inhibition*

Inhibitory control, as discussed earlier in relation to detour-tasks, is important for behavioral flexibility (Chow, Leaver, Wang, & Lea, 2017; Tebbich et al., 2010; Vlamings et al., 2010). Inhibitory control can be divided into motor inhibition, which is the inhibition of pre-potent motor responses and self-control, which is related more to the concept of patience. The latter is tested in studies where individuals can choose between an immediate small reward or a delayed larger reward (Evans et al., 2012; Kabadayi et al., 2018; Stevens, Hallinan, & Hauser, 2005). In their study of inhibitory motor control across 36 species, MacLean et al. (2014) found that absolute brain volume was the best predictor; *relative* brain size has been shown to correlate with innovation and tool-use rates and general cognitive ability as well (Deaner, Isler, Burkart, & Van Schaik, 2007; Overington et al., 2009; Reader & Laland, 2002; Reader & MacDonald, 2003). Others, like Stevens et al. (2005) argue that inhibitory (self-) control

is influenced by feeding ecology - species that hunt for prey or travel over large areas to eat a diverse array of food are more likely to be impulsive than those whose dietary constraints require patience (for example, the common marmoset - who feeds on exudates and must wait for gum to flow out of trees). Inhibitory control can be contrasted with perseveration or "the inappropriate repetition or maintenance of an activity or an abstract rule" which is a barrier to behavioral flexibility (Manrique & Call, 2015; Nilsson et al., 2015). In their study with captive Old and New World monkeys, Judge, Evans, Schroepfer, & Gross (2011) found that perseveration on a reversal learning task was associated with "self-directive behavior" indicative of anxiety and emotional arousal.

Despite the popular view that ecological generalism is related to behavioral flexibility, Malsburg & Fichtel (2018) found that a specialist mouse lemur species could outperform a generalist one on a multi-access-box task, which they claim is related to the enhanced inhibitory control found in the specialists. Sumatran orangutans (*Pongo abelii*) are more successful on physical cognition tasks than Bornean orangutans (*Pongo pygmaeus*), which is hypothesized to occur because of their enhanced inhibitory control (Forss, Willems, Call, & Van Schaik, 2016). Inhibition seems to be related to problem solving in some way. Dugatkin & Alfieri (2003) consider the possibility that inhibition influences the way individuals learn associations, which may itself mediate flexible behavior. However, it is important to note that inhibitory control may be context-dependent, so comparisons among studies with different contexts should be interpreted with caution (Amici et al., 2018; Brucks, Marshall-Pescini, Wallis, Huber, & Range, 2017). Furthermore, studies that focus more on innovation than behavioral flexibility are less likely to find an effect of inhibition, as persistence may be more important in these instances (Day et al., 2003; Johnson-Ulrich et al., 2018). Finally, as discussed earlier, it is important to keep in mind the limitations that come with various inhibitory control tasks; sometimes these tasks are more diagnostic of whether or not the individual is capable of detecting the fact that a certain response will prevent them

to obtain a reward, making other factors like causal reasoning and visual acuity, for example, necessary to solve these tasks (Kabadayi et al., 2018).

#### *2.3.1.3 Divergent thinking vs. functional fixedness*

Divergent thinking, or the ability to come up with different solutions to a single problem, is important for acquiring new strategies. However, because there is no standard measure of divergent thinking that can be used with animals, most studies of divergent thinking are strategy prevention paradigms: which test both the ability to come up with and acquire new strategies *and* the ability to abandon old ones, meaning that these tasks do not solely test divergent thinking per se. For example, in their recent study with chimpanzees (*Pan troglodytes*), Harrison & Whiten (2018) gave individuals an artificial foraging task that entailed retrieving juice from a tube using tools. Once individuals found effective strategies in the first phase, these strategies were prevented in the second phase. Although individuals were able to use a new solution in the second phase, they continued to use the previously successful solution for a majority of the time (at least 50%).

Harrison & Whiten (2018) argue that behavioral flexibility in chimpanzees is limited by their inability to abandon the previously successful strategies. However, the fact that individuals were able to use the tools in novel ways (even if they did not preferentially adopt these strategies) demonstrates that the individuals were able, to some extent, to think of novel ways to use the tools and interact with the task. In a recent study, Jacobson & Hopper (2019) presented chimpanzees and gorillas (*Gorilla gorilla gorilla*) with a causally transparent task which required the removal of straws in order to access food suspended in a clear tube. The individuals tried new strategies throughout the experiment and were able to switch to more efficient strategies when the conditions changed. Presumably, the capacity for divergent thinking is hard to accurately measure through strategy prevention paradigms, because of the additional influence of other factors. This highlights the importance of developing measures of divergent

thinking that can be used with animals, which could be similar to boxes used to test divergent thinking and curiosity in human infants (Banta, 1970; Hoicka et al., 2013).

#### *2.3.1.4 Physical and spatial cognition: representations and causal reasoning*

Understanding the relationships between physical objects in the environment is crucial to survival. In order to respond flexibly to changes in their surroundings, individuals must be able to perceive these changes accurately - which requires spatial and object representation as well as causal reasoning (Deaner, Schaik, & Johnson, 2006; Logan, 2016). Accurate mental representations of the environment, including the objects within it and the relationships between them are necessary not only for behavioral flexibility but also for problem-solving and foraging skills more generally. An ability to engage in causal reasoning, is also crucial to many forms of behavioral flexibility. Causal reasoning is often tested using contact vs. support scenarios, where the animal's ability to differentiate between these two relations is tested (Yamazaki, Iriki, & Watanabe, 2011). Differences in representations and the understanding of physical causation may be related to an individual's feeding ecology and prior experiences, discussed later (Platt, Brannon, Briese, & French, 1996). Furthermore, it has been suggested that advanced physical (and social) cognition is related to increased inhibitory control within a species (Sherwood, Subiaul, & Zawidzki, 2008).

The relevance of physical and spatial cognition can also be considered in concert with the fact that extractive foraging and other foraging behaviors that necessitate complex object manipulation and an understanding of the physical environment have been proposed as factors important to the evolution of intelligence in primates; this is commonly referred to as the extractive foraging hypothesis (Day et al., 2003; Parker, 2015). In addition to advanced physical cognition, Dunbar (1992, p. 472) speculates that animals will also "need to learn high-level cognitive rules that can be applied in a wide range of circumstances to different kinds of embedded resources," which suggests that these two factors may

have some sort of reciprocal relationship. Extractive foraging has also been associated with opportunism and neophilia (Day et al., 2003). Studying the associations between physical and spatial cognitive abilities, extractive foraging, personality, and flexible behaviors in other domains would increase understanding of how these various factors are related to behavioral flexibility, the development of material culture, and human evolution.

#### *2.3.1.5 Discrimination learning*

Discrimination learning, or the ability to respond differently to different stimuli, is an important aspect of behavioral flexibility. Discrimination can be achieved through several routes, including non-associative learning (like habituation), associative learning, and reasoning; crucially, it seems to entail two processes, 1) learning which dimensions and features of the stimulus need to be attended to - related to attention and appraisal, and 2) learning the appropriate response and attaching it to each relevant aspect of the stimulus - related to species and individual characteristics as well as personality traits that have an influence on habitual responding and associative learning (Bitterman, Sutherland, & Mackintosh, 1972). As Nilsson et al. (2015) describe, performance on tasks like reversal-learning and set-shifting depend highly on how the discriminations are acquired and Tebbich et al. (2010) discuss the importance of fast, effective learning by trial-and-error in correctly responding to novel situations. In their review of discrimination learning in animals, Sutherland & Mackintosh (1971) suggest that selective attention is the main mechanism driving discrimination learning. In their study of spatial discrimination learning (in terms of a reversal learning task) Rayburn-Reeves, Stagner, Kirk, & Zentall (2013) argue that increased attention to local feedback in rats (*Rattus norvegicus*) allows them to outperform parrots (*Columba livia*) which the authors further relate to the foraging ecology of each species and possible differences in personality.

Although not conducted on animals, studies by Beesley and colleagues on exploratory attention and (associative) learning in humans are very relevant here (Beesley, Nguyen, Pearson, & Le Pelley, 2015; Easdale, Le Pelley, & Beesley, 2019). They discuss the contrast between two ways of characterizing attention: "attentional exploitation" - where attention is guided by the "relative predictiveness" or informative value of the stimuli - and attentional exploration - where cues and stimuli whose consequences are unknown are more likely to be attended to (Beesley et al., 2015). Exploratory attention allows us to discover new contingencies in the environment, and the authors claim that this type of attention is relatively more sensitive to changes in context than attentional exploitation; actually, this is very similar to what is understood as perceptual curiosity. Using eye-tracking measures, Easdale, Pelley, & Beesley (2017) looked at reactions to sudden vs. stable conditions of uncertainty (expected vs. unexpected uncertainty) and found that participants who experienced sudden, unexpected uncertainty were faster at learning novel associations and increased their attention towards the cues within them. They conclude that exploratory attention, differing contexts, and various *types* of uncertainty all influence learning. This is interesting when considered alongside Croston et al.'s, (2017) study on mountain chickadees; individuals from "predictably harsh" environments perform poorly on a reversal learning task. Because behavioral flexibility entails adaptive responses to changing circumstances and contingencies, and unexpected uncertainty (when compared to expected uncertainty) leads to faster learning of novel contingencies in humans - it is plausible to assume that subtle variation in the context and nature of experiences with uncertainty has an effect on animal learning and behavioral flexibility.

#### *2.3.1.6 Categorization and concept learning*

The use of abstract concepts and the ability to categorize experiences and stimuli based on various characteristics can aid in behavioral flexibility. Many forms of behavioral flexibility require the

application of prior knowledge to "novel situations with the same underlying problem," which can be aided by stimulus generalization (Tebbich et al., 2010). Zentall, Wasserman, & Urcuioli (2014) summarize the three most important types of concept learning found in animals: perceptual/similarity based, relational, and associative. Perceptual or similarity-based concept learning, based on stimulus generalization and discrimination, entails grouping stimuli together based on their physical properties. Relational concept learning is based on the relationships among or between different stimuli. These types of concept learning are relevant to instances of behavioral flexibility where the individual comes across or is provided with a novel variant of something (e.g. tool or foraging problem...) that is familiar to them (eg. Hrubesch et al., 2009; Snowdon & Roskos, 2017; Vale et al., 2016)

Associative concept learning, on the other hand, is not based on physical properties or relationships, but instead is made possible through making associations between arbitrary stimuli based on prior experience. Examples of this include the use of food or alarm calls in non-human animals and language in humans (Zentall et al., 2014). Zentall et al. further discuss the creation of "associative classes" where various stimuli are arbitrarily grouped together because of some association between them. In addition to the fact that many experimental measures of behavioral flexibility require associative learning (eg. reversal-learning and set-shifting), associative concept learning also allows the animal to learn and keep track of various contingencies that relate to different aspects of their lives. Veit, Pidpruzhnykova, & Nieder (2015) demonstrate, in crows (*Corvus corone*), that associative learning allows for the creation of goal-directed representations in relation to novel and familiar stimuli which is mediated by the response that is required. Here, the crows seem to create two 'associative classes' – images that require response a (touching the red triangle) or response b (touching a blue square) in order to receive reward.

On the other hand, associative learning can also lead to conservatism or functional fixedness. This can be seen in the floating peanut task – where individuals can retrieve a peanut from a narrow

cylinder that is filled halfway with water by adding more water to it. Hanus, Mendes, Tennie, & Call (2011) found that chimpanzees would use new water sources to fill the tube but were unable to use their usual water bottle for this function. The authors speculate that because the chimpanzees associate their water bottle with drinking – functional fixedness occurs. If the water bottle is in the "associative class" of materials that provide nourishment, for example, individuals may have trouble removing it from this group and viewing it as a tool or as a means to retrieve a reward.

### 2.3.2 Personality

In the context of animal studies, personality can be defined as consistent individual differences in behavior and physiology that are "stable over time and across different contexts or situations;" it has also been studied under several other terms, including "temperament, behavioral syndromes, coping styles, or predispositions" (Carere & Maestripieri, 2013, p. 1). In the past decade, the ecological and evolutionary consequences of personality have started to be discovered and many have emphasized the interaction between personality and cognition (Carere & Locurto, 2011; Sih & Del Giudice, 2012). Several authors have also looked at the relationship between personality and behavioral flexibility; Guido, Biondi, Vasallo, & Muzio (2017, p. 591) summarize this relationship nicely: "an individual's personality type can limit the extent to which the individual might behave flexibly, by influencing the way an individual pays attention to novelty and how much information it collects and stores, which in turn affects the individual's decision-making and learning process." Duckworth (2010, p. 752) argues that "intrinsic constraints to behavioral flexibility due to time, energetic, or functional constraints" might explain why some personality traits are present in an individual, and claims that they are crucial to the evolution of personality. Mathot et al. (2012) emphasize the importance of observing responses to uncertainty in order to understand personality and behavioral flexibility in animals.

Personality in animals is studied through the observation of variation in aggression, reactivity, exploratory behavior, general activity levels, sociability, and responses to novelty (Dall, 2004). These traits seem to correlate with one another and with cognitive style in many instances, and have been classed together in two broad groups - slow vs. fast (Brust, Wuerz, & Krüger, 2013; Réale et al., 2010). Because of the central roles of responses to novelty and motivation in behavioral flexibility, I will first discuss these factors and then move on to the two broad groups of traits that are characterized as animal personality measures.

#### *2.3.2.1 Neophobia, neophilia, and curiosity*

Because behavioral flexibility is related to an animal's response to new or changing conditions, it is unsurprising that reactions to novelty are a major component in studies of behavioral flexibility. Attention is most readily directed to novel stimuli, and novelty has been considered as an important component of appraisal (Berlyne, 1950; Biondi, Guido, Bó, Muzio, & Vassallo, 2015; Faustino et al., 2015). Although neophobia and neophilia are often portrayed as two ends of a continuum, they are not opposites. Furthermore, as Bergman & Kitchen (2009) emphasize, it is hard to measure neophobia based on behaviors toward novel objects or tasks, as an individual may be very scared of a novel item but nevertheless be inclined to approach it because they are attracted to it (neophilia). For example, Byrne (2013) describes a chimpanzee who is observing a man-made fire, which he chooses to investigate with a little stick, despite the fearful look on his face.

Neophobia can be defined as an "ecologically relevant fear behavior that arises through a cognitive assessment of novel stimuli" (Greggor, Thornton, & Clayton, 2015, p. 82). Neophobia has been reported to be negatively associated with reversal-learning performance (Guido et al., 2017; Tebbich, Stankewitz, & Teschke, 2012) but has also been identified as a predictor of behavioral flexibility in the wild (Herborn et al., 2014). It is also possible for individuals to display both high neophobia and

neophilia, like the wolves (*Canis lupus*) in Moretti, Hentrup, Kotrschal, & Range's (2015) study of reactions to novelty. Likewise, Sabbatini, Stammati, Tavares, & Visalberghi (2008) claim that neophilia and neophobia are independent responses motivationally after finding that tufted capuchins (*Cebus libidinosus*) are attracted to novel foods and will spend a great deal of time exploring them (neophilia) but are unlikely to eat them (neophobia) when compared to familiar foods. Reader (2015) argues that individuals with high neophobia are likely to disengage and re-engage with a task quite rapidly, which may lead them to realize, attend to, or manipulate different parts of the novel object or situation. On the other hand, individuals with high neophilia are more likely to approach, attend to, or manipulate novel objects. Therefore, a combination of high neophilia and neophobia- like in ravens (*Corvus corax*) who are attracted to novelty but avoid it - may actually lead to higher behavioral flexibility (Reader, 2015).

In contrast to neophobia, neophilia is closely related to curiosity. Tebbich et al. (2012) argue that the "seeking of novel information" is crucial to behavioral flexibility. Berlyne, perhaps the most notable investigator of curiosity, claimed that there are two kinds of curiosity. "Epistemic curiosity" refers to curiosity about information or facts, or a desire for knowledge. "Perceptual curiosity" refers to curiosity about physical objects, especially towards novel stimuli (Berlyne, 1955). As discussed earlier, Jepma et al. (2012) found that perceptual curiosity in humans was associated with increased neural activity in areas related to motivation, rewards, and recall ability. Kidd & Hayden (2015, p. 450) define perceptual curiosity as "the driving force that motivates organisms to seek out novel stimuli." Accordingly, Damerius et al. (2017) assessed orangutans on several problem-solving tasks designed to test physical cognition; the only reliable predictor of problem-solving performance was curiosity. Although there is little empirical evidence on the relationship between curiosity and behavioral flexibility, it is clear that at least some of the underlying factors related to the two concepts are shared.

#### *2.3.2.2 Motivation*

Motivation, usually discussed in relation to instincts or an internal, biologically determined drive, is related to the generation of behavior, how the external environment influences the mechanisms that generate behavior, and how/why the behavior is beneficial to the individual (Colgan, 1989). As motivation is necessarily related to virtually all aspects of animal life and behavior, it is unsurprising to find that numerous studies point to motivation as a predictor of success on behavioral flexibility measures (Malsburg & Fichtel, 2018); and, as van Horik & Madden (2016, p. 196) claim, differences in task performance may be related to "inherent motivational differences *alone*." As discussed earlier, motivation to retrieve food from a task, for example, may have important consequences on whether or not the task is attended to and solved (Ebel & Call, 2018). However, in the context of behavioral flexibility, motivation is usually discussed in relation to novelty. For example, in their study of behavioral flexibility and innovation in wild red-fronted lemurs (*Eulemur rufifrons*), Huebner & Fichtel (2015) report that a general interest in novelty and motivation to approach it is an important basis for success in innovative-problem solving tasks.

#### *2.3.2.3 Exploration, activity, and reactivity: the proactive-reactive, shy-bold, and slow-fast continuums*

Closely related to the terms discussed so far, exploration can refer to any information-gathering activity and exploratory tendencies have been studied and understood as a marker of personality that influences behavioral flexibility (Biondi et al., 2015; Guillette, Reddon, Hurd, & Sturdy, 2009; Mangalam & Singh, 2013; Mettke-Hofmann, Wink, Winkler, & Leisler, 2005).[4] Discussed more commonly as 'personality' measures themselves (especially in avian species), the shy-bold and proactive-reactive

[4] See Biondi et al. (2010) for an explanation of how exploration and neophobia are shaped by different selective forces.

continuums are closely related to an animal's exploratory behavior, and have also been discussed as predictors of behavioral flexibility (Bolhuis, Schouten, Leeuw, Schrama, & Wiegant, 2004; Coppens et al., 2010; Lermite, Peneaux, & Griffin, 2017). These measures have been linked together to form two broad groups: bold individuals are characterized as being more aggressive, physically active, exploratory, and proactive (manipulate situations instead of reacting to them), than shy (reactive) individuals (Carere & Locurto, 2011; Griffin, Guez, Lermite, & Patience, 2013; Monestier et al., 2017). Sih & Del Giudice (2012) discuss these two groups in relation to cognitive styles - "the way individuals acquire, process, store or act on information, independent of cognitive ability." They speculate that there is a speed-accuracy tradeoff in cognitive styles, with "fast" individuals having high speed but low accuracy and "slow" individuals having a low speed but high accuracy (but see Raine & Chittka, 2012) This has further been linked to pace-of-life syndromes, by Réale et al. (2010, p. 4053; Figure 1).

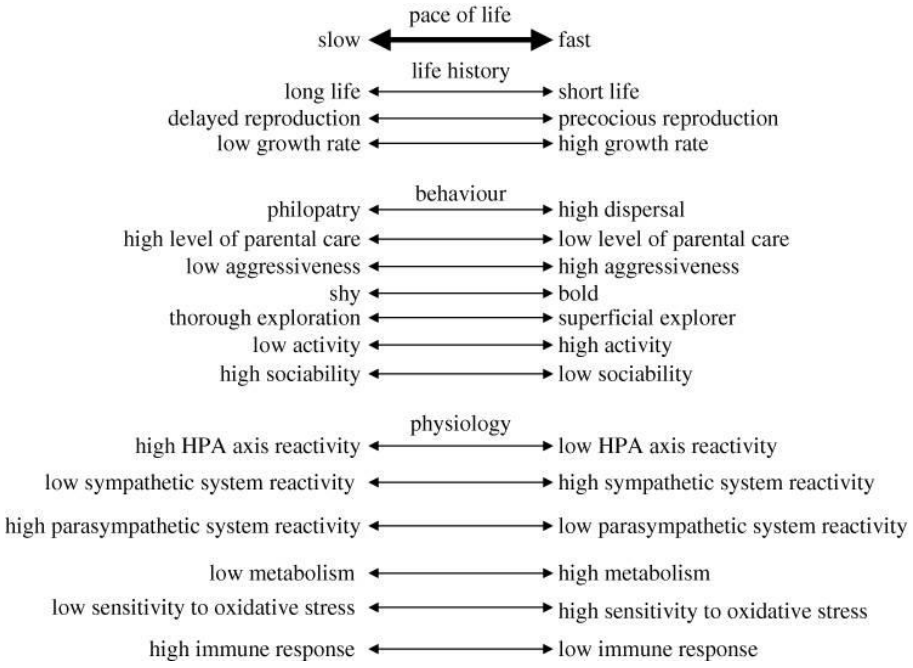



*Figure 1 – Figure from Reale et al. (2010, p. 4053) linking the "pace of life" continuum to aspects of life history, behavior, and physiology*

It is important to note that not only the *amount* of exploration but also the *kind* of exploration an individual engages in is crucial for behavioral flexibility. Overall, animals who display higher rates of exploratory behavior and are faster to explore novel environments perform better in various problem-solving tasks, presumably because they are faster learners (Dugatkin & Alfieri, 2003; Light, Grossman, Kolata, Wass, & Matzel, 2011; but see Lermite et al., 2017 for issues with measures of exploratory behavior). However, the ways in which exploratory tendencies impact behavioral flexibility tasks are quite nuanced, as individuals who are faster at learning are not always the most flexible (Guido et al., 2017; Logan, 2016a). As Titulaer, van Oers, & Naguib (2012) describe in their study of fast and slow exploring birds, fast (proactive) explorers are primarily guided by internal cues, rather than environmental ones, and explore their surroundings quickly and superficially. On the other hand, slow (reactive) explorers examine their surroundings more thoroughly and are more sensitive to external cues - which has been described as a strategy to reduce uncertainty (Arvidsson & Matthysen, 2016; Mathot et al., 2012). Although the fast explorer may perform better on some tests of behavioral flexibility (because of their readiness to quickly approach and manipulate novel items), it is possible that the slow explorer is more successful in naturalistic settings that require patience and attention to detail (see Malsburg & Fichtel, 2018, p. 18 for an example). This is related to the finding that high general physical activity level is associated with enhanced problem-solving abilities but lower success in reversal learning tasks (Brust et al., 2013; Johnson-Ulrich et al., 2018; Sih et al., 2004; Sih & Del Giudice, 2012). Carere & Locurto (2011) speculate that bold individuals are more successful on completely novel tasks, while shy individuals are more sensitive to changes within a familiar task; different traits have different advantages in different contexts.

The problem here is that these “personality measures,” which are often discussed in relation to exploration, are actually combining several characteristics that arguably should be measured separately

and more precisely. This is especially true when one considers that other factors (like age and sex differences) and the context may impact the interaction between exploratory tendencies/personality and performance on measures of behavioral flexibility. For example, Titulaer et al. (2012) found that fast-exploring male and slow-exploring female great tits (*Parus major*) performed better on a complex set-shifting task than their slow male and fast female counterparts. In order to gain a better understanding of how all of these factors interact, individual measurements of relevant factors (like exploration rate and type) in relation to performance on multiple tests of behavioral flexibility are required to discern the differential effects of these factors on different components of behavioral flexibility. In other words, the use of the more general fast-slow distinction is not particularly useful in studies of behavioral flexibility but may become more useful once we gain a better understanding of *how* these different aspects are related to one another and different displays of behavioral flexibility.

### 2.3.3 Individual Characteristics

Individual characteristics, like age, sex, and social status, have been shown to correlate with flexible behavior (Bunnell, Gore, & Perkins, 1980; Jones, 2005; Sabbatini et al., 2008; Simon, Gregory, Wood, & Moghaddam, 2013). However, there are no consistent findings (both within and among species) to suggest *how* these factors relate to behavioral flexibility. It has been suggested that characteristics like sex, age, or social status are not predictors themselves, but rather are associated with other underlying influential factors; for example, hormonal influences and reproductive status, the stage of development of the body (morphology) and brain (neural), and personality traits (Biondi et al., 2015; Lourenco & Casey, 2013; Westbrook et al., 2018). Furthermore, it is likely that the effect of these characteristics on behavioral flexibility are mediated by contextual factors and the task/behavior being

employed/observed. Using multiple measures of behavioral flexibility in varying populations and settings can help us better understand these effects.

#### *2.3.3.1 Sex*

Sex differences in behavioral flexibility are hard to detect. In their review of primate innovation, Reader & Laland (2001) found that innovation rates were higher in males; a finding that is in direct conflict with the popular view that females are more innovative. In their study of reversal learning in guppies (*Poecilia reticulata*), Lucon-Xiccato & Bisazza (2014) found that male guppies made twice as many errors as females while trying to learn the reversed contingency. The authors speculate that this difference in flexibility may be related to differences in mating strategies between males and females. On the other hand, Brust et al. (2013) found that male zebra finches (*Taeniopygia guttata*) were more successful than females on a reversal learning task. As discussed earlier, some studies have shown that the sex of the individual may determine the way in which their "personality" impacts their behavioral flexibility (Titulaer et al., 2012). Others demonstrate that various factors (for example, prenatal infection or early life stress) differentially effect flexible behaviors in males vs. females (Kunzler, Braun, & Bock, 2015; Zhang, Cazakoff, Thai, & Howland, 2012). Other studies fail to find any link between sex and behavioral flexibility (ex. Bergman & Kitchen, 2009; Boogert, Monceau, & Lefebvre, 2010; Kozlovsky, Branch, & Pravosudov, 2015). It is likely that the effects of sex that we find in studies of behavioral flexibility are influenced by the paradigm used or the behavior that is observed to test flexibility. Therefore, commenting on sex differences at the broad level of behavioral flexibility is not very useful.

#### *2.3.3.2 Age*

Although age influences an individual's propensity for behavioral flexibility, the nature of this relationship is not entirely clear. In their long term study of capuchin monkeys (*Cebus capucinus*), Perry, Barrett, & Godoy (2017) found that older individuals were more likely to invent novel social behaviors,

but younger individuals were more likely to invent new behaviors related to foraging, exploration, and self-comfort. In their review of innovation studies in primates, Reader & Laland (2001) found that adults are more innovative than juveniles. Similar results have been found experimentally in callitrichids (Kendal, Coe, & Laland, 2005) and meerkats (Thornton & Samson, 2012), but this may be due to maturational constraints on neural and motor activity (Lourenco & Casey, 2013). On the other hand, some authors stress the possibility that if "innovative" or novel behaviors are not adopted during the earlier stages of life, individuals will be unable to adopt them later in life (Biro, Carvalho, & Matsuzawa, 2010; Matsuzawa, 2007). These studies focus on innovation; as is the case for sex differences - it is likely that the effect of age on behavioral flexibility is influenced by the paradigm used or the behavior that is observed to test "flexibility."

Results obtained using other experimental paradigms have also been mixed. Westbrook et al. (2018) found that juvenile rats were more successful than adult rats in a reversal learning task and responded more efficiently to changes in reward value. However, performance on a set-shifting task was similar across the two groups. Guido et al. (2017) discuss that the reversal of learned reward contingencies is much faster in younger compared to older mammals. However, Weed, Bryant, & Perry (2008) found that juvenile macaques (*Macaca mulatta*) were not as successful as adults in a series of reversal learning and set-shifting tasks, which the authors relate to the ongoing development of the frontal cortex. After presenting 43 individuals of different great ape species to a reversal learning task, Manrique & Call (2015) found a U-shaped relation between age and perseverative responding, suggesting that elderly and infant animals are less flexible than their middle-aged counterparts. In their study of mouse lemurs (*Microcebus murinus*), Picq (2007) tested individuals on a series of discrimination, reversal, spatial, and set-shifting tasks and found that elderly individuals were impaired in their executive functioning (set-shifting and reversal learning) and declarative memory abilities

(necessary for flexibly comparing and contrasting items in memory); the effects of aging on these aspects of cognition may help to explain performance differences across the lifetime.

In studies like these, which use experimental paradigms like reversal learning and set-shifting, the complexity of the task and the motivational state of the individual can lead to different results. On the other hand, studies that use foraging tasks or puzzle boxes are prone to finding differences with age that are related to differences in dexterity and motor behavior. Studies that observe reactions to novelty or necessitate approaching a novel object in order to succeed are more likely to be capturing age related differences that are based on neophilia, neophobia, exploratory behavior, and motivation - which are usually higher in younger individuals (Biondi et al., 2015; Massen, Antonides, Arnold, Bionda, & Koski, 2013).[5] However, it is also important to consider the possibility that the effects of age on behavioral flexibility may be mediated through other conditions like brain maturation, pubertal status, and motivational state (Westbrook et al., 2018). Overall, making assumptions about behavioral flexibility based on age alone is unlikely to be useful.

#### *2.3.3.3 Social status*

In societies which actively maintain dominance hierarchies, social ranking can also have an effect on behavioral flexibility. In their study with wild starlings (*Sturnus vulgaris*), Boogert, Reader, & Laland (2006) found that the most dominant individuals were the fastest to solve an extractive foraging task. This is in line with the view that social rank is associated with more advanced cognitive abilities, and presumably, enhanced behavioral flexibility. However, it is also possible that individuals with lower social rank must adapt or inhibit their behavior more often in order to gain access to resources and activities that are usually dominated by their more highly ranked counterparts, with implications for

[5] Neophobia and problem-solving ability had a negative correlation in juvenile birds but no relationship when studied in adults (Biondi et al., 2010).

behavioral flexibility. For example, Bugnyar & Kotrschal (2004) discuss the novel and manipulative behavior of a subordinate raven (*Corvus corax*) who distracts a dominant conspecific from a food source by attracting the dominant's attention with a distraction and subsequently exploiting the food source himself. In their study of social learning in wild lemurs (*Lemur catta*), Kendal et al. (2010) found a positive relationship between task success and social rank. However, when looking at the subgroup of successful individuals, they found a negative relationship between rank and how *quickly* the task was solved.

In an early study, Bunnell & Perkins (1980) looked at the effects of social rank on problem solving ability in crab-eating macaques (*Macaca fascicularis*). They found that, when separated, low-ranking individuals were more successful than high-rankers in a reversal learning task, both in terms of acquiring the initial association and in the reversal. In a review, Reader & Laland (2001) suggest that lower-ranking individuals are more innovative and better at solving novel tasks than their higher-ranking counterparts. However, several studies have shown the opposite effect (Boogert, Reader, Hoppitt, & Laland, 2008; Drea, 1998). Some studies even suggest that mid-ranking individuals are most innovative (Russon, Kuncoro, Ferisa, & Handayani, 2010). It is possible that social rank doesn't have a direct influence on behavioral flexibility, but is moderated by another characteristic, like neophobia, motivation, or age (Wergård, Westlund, Spångberg, Fredlund, & Forkman, 2016). Interestingly, Guinote, (2007) argues that, in humans, "power" or the ability to influences others or control their outcomes is a determinant of increased "attentional flexibility" and inhibition; this may have something to do with the link between social status and behavioral flexibility in animals.

### 2.3.4 Contextual factors

Surrounding context will inevitably have an effect on an individuals' cognition and behavior, with the current popular view being that individuals from more complex, unpredictable or variable

environments are more likely to demonstrate flexible behaviors; experience with a wide range of conditions and contingencies that are constantly changing prepares the individual for flexible responding in the future (Rosati, 2017; Roth, LaDage, & Pravosudov, 2010; Tebbich & Teschke, 2014). Here, the literature relating context and behavioral flexibility is reviewed.

#### *2.3.4.1 Prior knowledge and experience*

Prior knowledge and experience can fundamentally affect an individual's behavioral flexibility in several different ways. For example, Grieco, Van Noordwijk, & Visser (2002) found that blue tits adjusted the timing of laying their eggs according to the food availability they had experienced in the previous year. Reader (2015) claims that prior experiences have an impact on the individuals' appraisal mechanisms and the way they look for and assess alternatives. On the other hand, after testing chimpanzees on an extractive foraging-like task, Hrubesch et al. (2009) argue that the prior mastery of a skill prevents individuals from exploring new ways of solving the task. Through functional fixedness, prior knowledge and experience can prevent behavioral flexibility.

In one sense, prior experience with novelty or complex environments can increase exploratory behavior and decrease neophobia (Berlyne, 1955). For example, Mangalam & Singh, (2013) found that 'temple' macaques (*Macaca radiata*), who spent more time exposed to humans (and, consequently, novel, non-natural objects) were more successful in a food extraction task than 'roadside' macaques who had little experience with humans and artificial objects. Biondi et al. (2015) explain that prior experience promotes exploration because it changes the individuals' perceptions of uncertainty and the value of the information that may be obtained through exploration. The effect of prior experiences on behavioral flexibility may also be mediated by the impact it has on inhibitory control. Fagnani, Barrera, Carballo, & Bentosela (2016) tested shelter and pet dogs on an A-not-B task in order to look at the effects of previous experience on inhibitory control. They found that shelter dogs had significantly

poorer performance compared to pet dogs, arguing that interaction with humans gives animals the experiences necessary to learn to inhibit behaviors. It is also possible, however, that there is a greater risk for shelter dogs that resources will not appear again if they wait. This is also related to prior experience in terms of feeding ecology.

Finally, Yamazaki, Iriki, & Watanabe (2011) argue that prior experience can aid individuals' in developing their understanding of physical causation. Hauser, Santos, Spaepen, & Pearson (2002) compared the performance of two groups of cottontop tamarins (*Saguinus oedipus*) on a means-ends problem solving task where individuals had to choose the correct cloth in order to retrieve a food reward being supported by it. One group had already participated on previous tool-use experiments and had learned to choose tools based on relevant characteristics (shape, material, orientation), while the other group consisted of naive individuals. Hauser et al. (2002) claim that the experienced individuals were more successful than the naive individuals because they were able to attend to the relevant characteristics of the task - the physical and causal relationships between the objects and the food reward. Prior experience with objects or tools seems to enhance the individual's understanding of physical causation; and this may be retained over long time periods (Vale et al., 2016).

#### *2.3.4.2 Stress: early life, acute, and chronic*

As it does in humans, stress due to various adverse circumstances during the early years of life can lead to cognitive and emotional deficits which negatively affect behavioral flexibility in animals (Harms, Bowen, Hanson, & Seth, 2018; Hedges & Woon, 2011). For example, studies have shown that common marmosets (*Callithrix jacchus*) deprived of contact with conspecifics in infancy (a cause of early life stress) are impaired in detour tasks of behavioral inhibition, reversal-learning tasks, and in their ability to regulate their emotions through positive social interaction (Dettling, Feldon, & Pryce, 2002; Pryce, Dettling, Spengler, Spaete, & Feldon, 2004). In a review, Pryce et al. (2005) discuss the

"depression-like" effects of early life stress in non-human animals: decreases in motivation for reward, an inability to cope with difficult situations, and changes in physiology – all of which are relevant to flexible behavior. However, as Gapp et al. (2014) discuss, in some cases early life stress may have positive effects by fostering lower stress reactivity and the ability to respond adaptively towards future stressors. They found that the adult offspring of mice who had experienced early life stress were actually more successful on a series of tasks that required goal-directedness and flexibility. The authors note that varying types and levels of severity in early life stress seem to have distinct influences on behavioral flexibility in individuals and their offspring; they emphasize the fact that the severity of early life stress or adversity cannot simply be assumed to have a linear relationship with negative or positive effects on flexible behavior.

Acute stress, which is most commonly [studied] in laboratory studies, also seems to have an effect on behavioral flexibility (Maille & Schradin, 2017). In their review on the effects of acute and chronic stress on reversal learning and set-shifting in rodents, Hurtubise & Howland (2017) conclude that: "*Acute and short-term repetition of stress appears to facilitate reversal learning whereas the longer term repetition of stress impairs reversal learning. Stress facilitated intradimensional set-shifting within a single, short-term stress protocol but otherwise generally impaired set-shifting performance in acute and repeated stress paradigms. Chronic unpredictable stress impairs reversal learning and set-shifting whereas repeated cold intermittent stress selectively impairs reversal learning and has no effect on set-shifting*." Stress has also been found to have a positive relationship with neophobia (Monestier et al., 2017). Future work on the effects of early life, acute, and chronic stress in more ecologically valid settings will provide further understanding of how stress influences behavioral flexibility in the wild. This is a crucial variable especially in work with captive animals, where conclusions about the effect of species are made without controlling for the impact of stress.

#### *2.3.4.3 Audience effects*

The presence of an audience can also influence behavioral flexibility (Otani, Sawada, & Hanya, 2014). Cronin, Pieper, Van Leeuwen, Mundry, & Haun (2014) tested chimpanzees (Pan troglodytes) on a "novel resources acquisition task," alone and in a pair with an individual from their social group. Individuals stood on top of a mesh tower, with a small baited tray hanging below them - suspended by two chains. By pulling the two chains upwards equally, they could gain access to the food. When tested alone, individuals spent significantly longer trying to (successfully) access the food. Furthermore, some individuals who had successfully retrieved the reward when alone, did not do so when given the opportunity in a pair. The authors argue that this may be due to the possibility of food competition - as some trials included contact and non-contact aggression. By inhibiting the new behavior, the participating individual (especially low-ranking) can avoid a negative encounter; in a way that is not necessarily being measured by the task, the individuals are behaving flexibly, on the basis of who is watching them.

On the other hand, the presence of conspecifics can also increase the possibility of the adoption of new behaviors through social facilitation. In their study with capuchin monkeys (*Cebus apella*), Dindo, Whiten, & de Waal (2009) found that individuals who were introduced to a novel foraging task in the presence of a feeding conspecific learned the successful solution three times faster than individuals who completed it alone. The authors argue that, through social facilitation, the presence of a familiar, feeding conspecific increases the individual's motivation to explore the task. Likewise, the presence of conspecifics facilitated exploration of novel objects in dogs (*Canis familiaris*) and wolves (*Canis lupus;* Moretti et al. 2015).

Similar to what is observed in human infants, Yamamoto & Lopes (2004) found that young captive marmosets *(Callithrix jacchus*) were less likely to engage with/eat novel foods when adults were absent. It is possible that social facilitation through the observation of adult models allows younger

individuals to overcome their initial neophobia towards novel foods. Moreover, individuals benefit from the presence of a skilled conspecific. In cotton top tamarins (*Saguinus oedipus*) individuals who attempted the task alone or with a naive conspecific showed high neophobia and low exploration of the apparatus while those who attempted it in the presence of a knowledgeable mate were much more likely to solve it (Moscovice & Snowdon 2006). As the knowledgeable individuals attend to the more salient features of the task, and the individuals being tested attend to their behavior - this facilitate success through local enhancement (Hoppitt & Laland, 2008). Knowledgeable individuals also provide a model of motor actions that may be necessary to solve the task (Voelkl & Huber, 2000).

#### *2.3.4.4 Metabolic rate, energy expenditure, and resource availability*

Metabolic rate - the rate at which an animal oxidizes substrates to produce energy - can vary both within and between individuals of different species. It can influence behavioral flexibility - as behavior and cognition are inevitably restricted by the amount of energy available to the individual (Careau et al., 2011). Furthermore, activities like exploration and innovation have high energetic costs, presumably making it less like likely for individuals with restricted energy to partake in them (Reader, 2015). In their review, Biro & Stamps (2010) look at studies that test the relationship between resting metabolic rate (RMR) and behavior in birds, fish, mammals, a crustacean, and an insect. They conclude that higher RMRs are indicative of higher energy outputs, and that RMR is correlated with consistent individual differences in behavior. Nilsson, Åkesson, & Nilsson (2009) use blue tits to show that RMR may be highly heritable, and Careau et al. (2011) use deer mice to show that there is genetic covariation between RMR and exploratory behavior. As Careau, Thomas, Humphries, & Réale (2008, p. 641) nicely summarize, “because activity, exploration, boldness, and aggressiveness are energetically costly, personality and metabolism should be correlated and physiological constraints may underlie behavioral syndromes.”

Differences in energy availability may also manifest in differences in motivation - especially towards food. In their study of a generalist and specialist species of mouse lemur, Malsburg & Fichtel (2018, p. 19) measure BMI as an indicator of energetic state. They argue that problem-solving performance may be related to energy expenditure. Individuals with a low metabolic rate and "narrow feeding niche" require higher rates of efficiency in their feeding behaviors, leading to higher motivation to retrieve food rewards. Huebner, Fichtel, & Kappeler (2018) found that the amount of time it took for grey mouse lemurs (*Microcebus murinus*) to solve an extractive foraging task and the probability that they would be successful was related to their BMI; individuals with lower BMI (mostly juveniles) were faster to solve the task, and successfully retrieved food rewards from more of the possible locations. Success on the task was also related to the amount of change in BMI over the winter - which lead the authors to speculate that this type of problem-solving may be relevant to survival in natural settings. Future studies that look at the relationship between energy expenditure and components of behavioral flexibility can help to determine how energetic constraints and metabolic rate influence flexible behaviors in varying contexts, species, and settings.

Also related to the energetic constraints of an individual, periods of food scarcity may also lead to flexible behavior. For example, recent anecdotal claims suggest that galapagos sea lions (*Zalophus wollebaeki*) have responded to long-term decreases in their usual food source, the small pacific sardines (*Sardinops sagax*), by learning to hunt yellowfin tuna (*Thunnes albacares*) which can swim twice as fast as the sea lions can (Stone, 2018). Harris, Chapman, & Monfort (2010) discuss the behavioral and physiological effects of food scarcity on wild colobus monkeys (*Colobus guereza*), who are able to adjust their behaviors in relation to what they eat, where and how they forage for it, and how far they are willing to go (in terms of distance) to find food resources.

Not only food scarcity, but also instability in available food sources may also impact behavioral flexibility. In their study of woodpecker finches (*Cactospiza pallida*) from unpredictable (variable food

availability) and stable habits, Tebbich & Teschke (2014) tested individuals from the two groups in terms of reactions to novelty, reversal learning, and a problem solving task (opening a box). They found that although there were no differences in problem-solving ability, the individuals from the unpredictable environment demonstrated faster reversal learning and a higher attraction to novelty (neophilia). These individuals were also more neophobic; this relates back to Reader's (2015) claim that high neophobia coupled with high neophilia may lead to more flexible behavior.

If one accepts the adage "necessity is the mother of invention," periods of food scarcity may lead to flexible behavior, as individuals' are forced to obtain new resources or find new ways to retrieve familiar resources in order to survive. Similarly, instability in terms of available food resources may also cause individuals to generate new behaviors and remain vigilant in order to obtain new or hard to obtain food resources. On the other hand, an abundance of food resources and a reduction in dietary constraints may afford the individual with free time and extra neural resources which could aid in flexible behavior. As Reader (2015) considers, energetically costly activities like exploration are less likely to occur in individuals that have a low energy reserve or have high energy demands. It seems that this tendency would be exacerbated in periods of food scarcity but diminished in periods of high food availability. This will be discussed in relation to the captivity effect.

#### *2.3.4.5 Reproductive status*

Reproductive status, especially in females, can also influence behavioral flexibility. As Miller, Bales, Ramos, & Dietz (2006) discuss, reproductive events (like pregnancy and lactation) can have a big influence on the amount of energy necessary for survival (McCabe & Fedigan, 2007). Furthermore, the aftermath of these events (especially infant carrying) may lead to higher risks of predation which necessitate higher vigilance levels. Moreover, these events may also limit the amount of resources the

individual can retrieve and consume, putting further restrictions on the energy available to the individual and, perhaps, making it more difficult for them to engage in flexible behavior.

It is also possible that individuals who are pregnant, or that have young offspring, are more likely to behave flexibly - in order to increase their energy intake and the likelihood of their offspring's survival. For example, Bodensteiner, Cain, Ray, & Hamula (2006) found that pregnancy was associated with enhanced behavioral flexibility in rats, as pregnant individuals demonstrated less perseveration to previously learned information and a quicker adoption of new information. Russon et al. (2010) describe spontaneous tool use in orangutan (*Pongo pygmaeus*) first-time mothers, who would use long sticks to test the depth of the water before entering it with their infants; they relate this to the increased "wariness" that results from first-time motherhood.

In another sense, reproductive state may influence behavioral flexibility by causing changes in cognitive and emotional processing related to hormonal influences on perception, learning, and memory in both males and females (e.g. Koebele et al., 2017; Ormerod & Galea, 2003). Hopper et al. (2014) found evidence suggesting that female chimpanzees are more successful in problem solving tasks in the period after estrus, when sexual swellings are subsiding. This is interesting when considered in relation to Leuner & Gould's (2010) finding that female rats have higher cognitive flexibility during the postpartum period due to neuronal growth in the medial prefrontal cortex.

The effects of reproductive status on behavioral flexibility can be indirectly explored by looking at the effects of being neutered on domesticated animals. Starling, Branson, Thomson, & McGreevy (2013) found that dogs who were neutered were rated as less bold than their non-neutered counterparts; they argue that the sexual capacity of the individual may have an effect on how individuals engage in social interaction and react to novelty. Finkler, Gunther, & Terkel (2011) found that, once neutered, cats were less likely to participate in aggressive or agonistic behavior. Comparing

neutered and sexually intact individuals on various tests of behavioral flexibility may aid in our understanding of how reproductive status plays a role in flexible behavior.

#### *2.3.4.6 Captivity effect*

Studies which consider the influence of captivity on the propensity for behavioral flexibility have yielded varied and sometimes directly conflicting results. In one sense, captivity seems to be detrimental to behavioral flexibility. For example, in their review of reintroduced golden lion tamarins (*Leontopithecus rosalia*), Beck et al. (1991) discuss deficits in locomotion and the ability to find food that seem to be caused by captive living; wild-born tamarins were more likely to survive once re-introduced. In their discussion of behavioral persistence in bears, Vickery & Mason (2003) argue that captivity can lead to problems with inhibition and stereotypic behavior, and subsequently reduce the individual's' capacity to behave flexibly in order to survive in the wild. Overall, captivity, and especially being reared in captivity, may cause reduced behavioral flexibility (Mason et al., 2013).

However, studies that focus on innovation, tool-use, and *some* problem-solving behaviors seem to show the opposite - captive animals perform well in these domains. Benson-Amram, Weldele, & Holekamp (2013) found that captive spotted hyenas (*Crocuta crocuta*) were more successful in an innovative problem-solving task (similar to multi-access box) than their wild counterparts. The same seems to be the case in orangutans (Russon et al., 2009). In many of the great ape species, captive individuals are more likely to use tools, or use tools more frequently than wild ones (Boysen, Kuhlmeier, Halliday, & Halliday, 2009; Gruber, Clay, & Zuberbühler, 2010). This has also been found in several other species including elephants, birds, and rats (Auersperg, Szabo, Von Bayern, & Kacelnik, 2012; Bird & Emery, 2009; Chevalier-Skolnikoff & Liska, 1993; Okanoya, Tokimoto, Kumazawa, Hihara, & Iriki, 2008). After observing two different types of tool use in eight captive golden lion tamarins, Stoinski & Beck (2001) argue that an “intermediate level of complexity” of the environment facilitated their novel usage

of objects for extractive foraging like actions - by providing ample opportunities for exploration and tool use while also eliminating factors that take up time, physical energy and neural resources in the wild (e.g. finding food, hiding from predators, travelling). More generally, it seems that exposure to anthropogenic objects and to humans more generally can enhance problem solving abilities in certain domains (Bering, 2004; but see Leavens & Bard, 2019 for discussions of captivity hampering cognition in animals).

The seemingly positive effect of captivity on curiosity, innovation, tool-use, and problem solving has been summarized by van Schaik et al. (2016) as the "captivity effect," which they discuss in relation to orangutans. In one sense, captivity provides animals with a safe environment, where food is guaranteed and the attentional resources and vigilance necessary for survival is relatively low. Related to this, while novelty in the wild is more likely to lead to danger, novel objects in captivity are usually provided by humans that the animals have had prolonged contact and experience with. It is likely that this leads to a decrease in neophobia. Observing human models may also lead to more exploration. Because the captive individual's "cognitive load" is lower, it is more likely that they will explore their environment for longer periods of time and with a greater degree of attention - which is afforded to them by the free time and neural resources gained in captivity. The authors argue that, in orangutans, captivity leads to an increase in creativity, curiosity, exploration, and innovation. They speculate that humans may have undergone conditions that are similar to those afforded to other animals in captivity now, with decreases in predation risk and the adoption of cooperative breeding allowing for more exploration and creativity. It is possible that, under the right conditions, captivity can lead to enhanced behavioral flexibility.

#### *2.3.4.7 Novelty and complexity*

The level of novelty and complexity afforded by the individual's *current* environment also seems to have an effect on behavioral flexibility (Griffin, 2016; Reader et al., 2016). Biondi et al. (2015) found that the complexity of novel objects did not influence latency to approach the objects but did increase the amount of time that caracas (*Milvago chimango*) explored the objects - demonstrating that these characteristics may influence behavioral flexibility by mediating changes in neophobia and motivation to explore. The authors also discuss the way complexity can elicit opposing reactions. The benefit of exploring a complex object might seem higher, as more information can be obtained from it. However, more complex stimuli are more likely to mask potential risks that may lead to increased neophobia (Biondi et al., 2015). Therefore, the novelty and complexity of what the animal is being exposed to is important to consider in experimental studies.

### 2.3.5 Species characteristics

Although there are differences among individuals, some conclusions can be made about the propensity for behavioral flexibility in different species. The species concept itself is not well defined (Zinner & Roos, 2014). Still, there are consistent differences between groups of different species in tasks and observations of behavioral flexibility, which are ultimately related to the physical characteristics than constrain a species' behavior. I will discuss characteristics that are widely shared within species that seem to have an effect on behavioral flexibility in various domains.

#### *2.3.5.1 Feeding ecology: dietary breadth, foraging patterns, and complexity*

Differences in feeding ecology, especially in terms of dietary generalists vs. specialists, have been consistently shown as predictors of differences in behavioral flexibility (Mettke-Hofmann et al.,

2005; Sol et al., 2002).[6] A great example of the effects of dietary generalism vs. specialism can be found in Bergman & Kitchen's (2009) study of responses to novelty in wild baboons (*Papio ursinus*), who are habitat and dietary generalists, and geladas (*Theropithecus gelada*), who have a highly specialized diet. Baboons showed higher neophilia and rates of exploration than the geladas - which the authors relate to their feeding ecology. Likewise, Russell, Buchmann, & Papaj (2017) report that generalist bees are more flexible in their pollen collection behavior than specialist bees.

In a study of associative learning, reversal learning, and novel problem solving, Leal & Powell (2012) found that lizards (*Anolis evermanni*), who, as a species, display stereotyped behaviors and are not known for advanced cognitive abilities, were successful at learning associations, reversing them, and using multiple strategies to retrieve a reward. They claim that although lizards do not have some markers of behavioral flexibility (high social complexity, or complex foraging patterns), they do possess others, like niche generalism. The authors argue that the use of a variety of different habitats has a reciprocal relationship with willingness to explore and use novel environments, which can help to explain the lizards' success on these measures of behavioral flexibility.

Similar results have been found with primates. For example, in their study of responses to novelty in captive common marmosets (*Callithrix jacchus*) and Goeldi's monkeys (*Callimico goeldii*), Addessi, Chiarotti, & Visalberghi (2007) point to differences in feeding behaviors to explain why the marmosets were more likely to approach and eat novel foods than the Goeldi's monkeys. The authors claim that while common marmosets are likely to exploit novel food resources in their small home range when their preferred foods have limited availability, Goeldi's monkeys can travel across their relatively larger home ranges in order to find a food sources that has familiar and preferred foods. Thus, in addition to being a dietary "specialist" or "generalist" the details of feeding ecology and consequent

[6] Interestingly, Brooks, Maia, Duffy, Hultgren, & Rubenstein (2017) argue that there is a reciprocal relationship between generalism and cooperation, which may be related to the positive relationship between social complexity and behavioral flexibility (discussed in the next section).

habitat range have an effect on behavioral flexibility (also discussed in relation to "unexpected uncertainty").

In another study, Platt et al. (1996) studied visuospatial memory abilities in golden lion tamarins (L*eontopithecus rosalia*) and Wied's marmoset (*Callithrix kuhli*), through a series of experiments to compare each species' ability to remember the location of baited food wells. In all tasks the marmosets outperformed the lion tamarins at short retention intervals (5 minutes) while the opposite was found for longer intervals (24 or 48 hours). These differences in the acquisition and use of spatial information can be linked to foraging ecology. The lion tamarins travel over large areas of land to find food (ripe fruit) and forage for prey and must wait for these resources to regenerate before they re-visit them. On the other hand, Wied's marmosets will identify gum trees within a small area and return to them throughout the day (because they renew quickly). Consequently, lion tamarins must navigate through patches of resources that are relatively far from one another and cannot be visited at points close in time, while the marmosets travel between locations that are close to one another within smaller time periods. Platt et al. (1996, p. 384) argue that the visuospatial learning and memory abilities of each species may be "specialized for tracking the spatiotemporal distribution of their principal foods."

The impact of feeding ecology on behavioral flexibility may also be mediated by its impact on inhibitory control. When given the choice between immediately getting a small reward or waiting for a larger reward, common marmosets (*Callithrix jacchus*) waited much longer than cotton-top tamarins (*Saguinus oedipus*), which the authors relate to feeding ecology (Stevens et al., 2005). The tamarins must be alert and attentive in order to trap insects - a task that requires impulsive actions. On the other hand, marmosets partake in tree-gouging and then wait for the exudate to flow out - which requires patience rather than impulsivity. With the same species, Spaulding & Hauser (2005) found that marmosets were better at learning to preferentially select the correct tool based on its functionally relevant features; they argue that the patience required by the marmosets' feeding ecology allowed

them to attend to the tools and assess the options more efficiently. Consequently, the evolution of self-control in each species may be directly related to their feeding behaviors (also discussed by MacLean et al., 2014). To summarize, in addition to what the animal eats (dietary breadth) and how they retrieve the resources that they need (foraging patterns), *where* the animal finds its resources and the characteristics (especially complexity) of those locations is also important; differences in spatial and temporal distribution of resources impact behavioral flexibility.

#### *2.3.5.2 Social dynamics and complexity*

The social dynamics of a species, and the complexity of their social groups and interaction has also been identified as a factor which may influence behavioral flexibility (Kamilar & Baden, 2014). Bond et al. (2007) used a serial reversal learning task to test corvids species with differing levels of sociality; they claim that social complexity was the primary environmental factor differentiating them, supporting the view that 'social complexity' and 'behavioral flexibility' are positively related. A study by Amici, Aureli, & Call (2008) lends support to the idea that the effect of social dynamics and complexity on behavioral flexibility is mediated through changes in inhibitory control. After testing several primate species varying in their social dynamics (fission-fusion vs. cohesive groups) on five inhibitory control tasks, Amici et al. (2008) conclude that enhanced inhibitory control is exhibited by species with fission-fusion dynamics and that this enhanced ability is more positively associated with their social dynamics/complexity than with genetic influences or feeding ecology.

Social complexity may also have an influence on behavioral flexibility independently of the effects it has on inhibition. Great tits (*Parus major*), who also have fission-fusion dynamics, have been described as innovative, flexible, adaptive, and opportunistic (Aplin et al., 2015, 2017). Borrego & Gaines (2016) tested captive carnivores with varying levels of social complexity: lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*) and tigers (*Panthera tigris*) on a puzzle-box to test

propensity for innovation. Leopards and tigers are largely asocial, while lions (egalitarian) and hyenas (hierarchical) have more complex social systems. As the authors expected, leopards and tigers (largely asocial species) were least successful in solving the puzzle box with spotted hyenas (hierarchical group living) were most successful followed by lions (egalitarian group living). It is possible that the additional neural resources necessary for keeping track of each individual's rank in a hierarchical society can explain the spotted hyenas' better performance on the task.

Overall, many different cognitive skills have been associated with different levels of social complexity, including spatial and temporal representation, memory, inferential and analogical skills, and domain-general cognition (Aureli et al., 2008; de Waal & Tyack, 2003). Interestingly, Dunbar and colleagues found that neocortex size was associated with social group size in primates, carnivores, and some insectivores (Dunbar & Bever, 2010; Kudo & Dunbar, 2001); Tschudin (1998) reports the same for dolphins. It is possible that increases in neocortex size afford individuals with greater inhibitory control which can help to foster complex social systems through the inhibition of inappropriate or uncooperative social behaviors (Bjorklund & Kipp, 2002). Presumably, this inhibition would allow animals to work together cooperatively, which can be important in situations where an individual needs the help of others to exhibit flexible behavior. Cooperation is a major component of behavioral flexibility in human beings - the same may be true for other animals (Fuentes, 2004; Hare, Melis, Woods, Hastings, & Wrangham, 2007).[7]

#### *2.3.5.3 Motor diversity and complexity*

Motor diversity, discussed earlier in relation to behavioral diversity may also influence behavioral flexibility, especially in relation to innovation, tool-use, and flexible behaviors that include objects. Griffin, Diquelou, & Perea (2014) presented Indian mynas (*Sturnus tristis*) with an extractive

[7] Brooks et al. (2017) argue that there is a reciprocal relationship between ecological generalism and cooperation.

foraging task consisting of four compartments and found that motor diversity was associated with a faster latency to solving of compartments that were furthest from them, and the number of compartments the individual solved. The authors argue that a greater variety of distinct motor actions in combination with associative learning can lead to foraging success in novel or changing situations. Likewise, Johnson-Ulrich et al. (2018) found that success on a multi-access-box, was associated with higher motor diversity in spotted hyena (*Crocuta crocuta*). In their study of seven avian species, Diquelou, Griffin, & Sol (2016) found that "motor flexibility" (calculated by the frequency and number of distinct motor techniques performed) was positively associated with the probability that an individual would succeed and lower latencies to success, on an extractive foraging task. They speculate that motor diversity and cognitive capacities have an important link, especially in terms of the effects of associative learning, causal reasoning, and behavioral inhibition on motor activity. Griffin & Guez (2014) argue that motor diversity is positively related to problem-solving more generally.

#### *2.3.5.4 Brain size*

After finding a positive relationship between relative brain size and innovation rates in primates, Reader & MacDonald (2003) discuss the use of brain size as a "proxy measure" for behavioral flexibility. After reviewing over 400 re-introduction events of many mammalian species, Sol, Bacher, Reader, & Lefebvre (2008) found that relative brain size was positively associated with survival and conclude that larger brains increase the probability of survival in novel environments. In an analysis of a majority of the bat species alive today, Ratcliffe, Fenton, & Shettleworth (2006) found that flexible species (in terms of foraging patterns) had larger relative brain sizes. More generally, larger relative brain size has also been linked to increased social complexity and innovation (Reader & Laland, 2002). On the other hand, others have argued that *absolute* brain size is a predictor of inhibitory control and cognitive ability (MacLean et al., 2014; Deaner et al., 2007). In a recent study, Hopkins et al. (2019 p. 18) report that

"general intelligence in chimpanzees is associated with total brain size, total gray matter volume, and overall and region-specific variation in cortical thickness." Others stress the importance of other characteristics of the brain, like the number of cortical neurons there are within the brain, or modularity and interconnectivity (Chittka & Niven, 2009; Roth & Dicke, 2012). Similar to its relationship with other concepts, there seems to be some effects of brain size on behavioral flexibility, but the nature of this relationship is not entirely clear.

## 2.4. Using the concept of behavioral flexibility

Currently, the concept of "behavioral flexibility" is used very loosely and in widely varying contexts and fields. Superficially, one could conclude that a lot of different species have displayed evidence of high "behavioral flexibility," including flies, wasps, rats, parrots, octopuses, primates, and humans (Bublitz, Weinhold, Strobel, Dehnhardt, & Hanke, 2017; Grabowska et al., 2018; Hurtubise & Howland, 2017; Rachwani, Soska, & Adolph, 2017; Silva & Melo, 2018; Stök et al., 2015). However, the ability of the parasitoid wasp to efficiently alter the components of its chemical defense mechanisms - towards predator ants of different species and sizes (Stök et al., 2015)- cannot really be meaningfully compared to the "pharmacologically manipulated" rat's ability to complete set-shifting and reversal learning paradigms under acute or chronic stress (Hurtubise & Howland, 2017); or to the parrot's use of alternative food sources and creation of larger flocks in periods of low fresh fruit availability in the wild (Silva & Melo, 2018); or an octopus' ability to perform well on an operant conditioning task administered through an LCD touch screen monitor (Bublitz et al., 2017). Is it really possible to compare behavioral flexibility in the visual discrimination abilities of flies (Grabowska et al., 2018) to the behavioral flexibility in sitting abilities of human infants (Rachwani et al., 2017)? A survey of studies of behavioral flexibility in many species indicates that behaviors used to describe behavioral flexibility, and paradigms and tasks that are used to test it, are dependent on different neural and physiological

mechanisms and are influenced by different traits (Audet & Lefebvre, 2017; Tello-Ramos et al., 2019). Identifying and understanding all of these factors and the relations between them is necessary for a more comprehensive and functional understanding of behavioral flexibility.

# 3 - Cooperative breeding, cognition, and common marmosets

The following section introduces cooperative breeding systems and their proposed influence on cognition in callitrichid monkeys; more specifically, in common marmosets (*Callithrix jacchus*) – the species utilized in my study (Chapter 4).

## 3.1 Cooperative breeding

Cooperative breeding can be broadly defined as a reproductive system where individuals other than genetic parents (alloparents) help to take care of and provision offspring - often ensured through the delayed dispersal of adults (Solomon & French, 1997). This type of reproductive system seems to have evolved separately in several lineages (Lukas & Clutton-Brock, 2012). Cooperative breeding is relatively rare, only 9% of birds, 2% of mammals, 1% of fish, and less than 1% of insects have been observed to engage in this type of system (Eggert, 2017). In mammals, cooperative breeding is associated with specific life history and behavioral traits (Burkart, 2008). In most cooperative breeding mammals, all group members are biologically motivated to promote the survival of the same offspring. As a result of the shared responsibility for offspring care, breeding females can produce more offspring as the costs of reproduction are distributed; which can lead to increased litter size, inter-birth intervals, and relatively large offspring (Burkart, 2008). The fact that older infants can be cared for by helpers while the mother attends to a new born also generally allows for a slower maturation process in both human and non-human animals (Hrdy, 2005). The physiological basis for cooperative breeding is still debated (Schradin et al., 2018), but the consequences of cooperative breeding, particularly in mammals, have been studied extensively.

One of these consequences seems to be an increase in tolerance and decrease in within-group competition associated with increased social tolerance, strong social relationships, and lower levels of aggression towards in-group members (Burkart, 2009). Because offspring survival is dependent on the

allomaternal care, breeders, especially females, are sensitive to how well, how often, and how many helpers are available to provision and care for their offspring (Burkart, 2009). Because of these characteristics, it has been suggested that, at least in primates cooperative breeding paves the way for enhanced social cognition and communicative abilities (Snowdon, 2001).

Cooperative breeding has also been linked to enhanced cognitive functioning more generally, usually referred to as the cooperative breeding hypothesis (CBH; Burkart et al., 2009; Hrdy, 1999, 2005, 2006). Hrdy (1999) argues that cooperative breeding was a main driver of human evolution, in particular to the development of the unique cognitive abilities that we have today. Crucially, this is similar to the way Kandel et al. (2016) describe the role of behavioral flexibility in human evolution. Burkart & van Schaik (2016) argue that the motivational mechanisms necessary for cooperative breeding, such as tolerance and prosociality, also facilitate cognitive performance, particularly in the social domain. Of the non-human primates, all species of callitrichids have cooperative breeding systems.

## 3.2 The callitrichids

The callitrichidae (coming from the Greek kallitrikhos: "having beautiful hair") are a family of arboreal New World Monkeys consisting of the tamarins (*Saguinus* and *Leontopithecus*) and marmosets (*Callithrix*, *Cebuella*, *Callimico*, and *Mico*) who are characterized by their small social groups, high occurrence of twin births, cooperative breeding, food sharing, complex diets, small body sizes (<900g), and high predation pressures (Buckner, Lynch Alfaro, Rylands, & Alfaro, 2015; Garbino & Martins-Junior, 2018; Moro-Rios, Meyer, Silva-Pereira, & Ludwig, 2018; Price & Feistner, 1993; Siani, 2009; Slack, 2014). Unfortunately, a large portion of the callitrichids' natural habitats have been either degraded or destroyed due to human activity (Marsh, 2003). Still, there is wide variability in the conservation status of species both within and between genera; some species are considered to be in the IUCN category of "least concern" (ex. *Callithrix jacchus*) while others are critically endangered (ex. *Saguinus oedipus).*

In addition to being cooperative breeders (discussed below), callitrichids make good study species for two main reasons. 1) practically-speaking, callitrichids are small which makes them relatively easy to house and work with in captivity. Entering enclosures is not usually dangerous for the experimenter and the building and design of apparatuses does not require durable and costly material as it might for other species, such as great apes. 2) Various species of callitrichids are highly similar in many social and physical characteristics but also have slight differences, in feeding adaptations or group structure for example, which allows for the investigation of the effects of these differences on other characteristics (such as cognition or personality).

## 3.3 Cooperative breeding and cognition in callitrichids

All callitrichid species observed so far engage in allomaternal care through carrying and provisioning of offspring, sharing vigilance and cooperatively defending the group (Brown, Almond, & Bergen, 2004). Callitrichids live in family groups consisting of the breeding pair; helpers are not reproductively active themselves and are motivated to care for any infant regardless of relatedness (Zahed, Prudom, Snowdon, & Ziegler, 2008). Furthermore, as Burkart, Hrdy & van Schaik (2009, p. 179) point out, callitrichid offspring will spontaneously approach allomothers, suggesting that "benevolent attention" and "effective allomaternal care" over time must have selected for this motivation to self-transfer from parents to other adults in infants.

Many of the characteristics of cooperative breeding appear to influence callitrichid cognition and behavior. Callitrichids engage in cooperative provisioning, where offspring receive direct food offers from adults other than their parents (Rapaport, 1999). Fruit or prey is shared, which is initiated either by the begging of an infant or by food-offering vocalizations emitted by adults. Food provisioning can also provide immatures with information about what foods can be eaten and how they can be obtained – a form of "information donation" (Burkart, 2009, p. 136); this is one way that cooperative breeding

requires coordination and communication between individuals. Furthermore, sharing food requires the individual to inhibit the prepotent motor response to eat the food item themselves. Theoretically, therefore, cooperative breeding may also be associated with increased inhibitory control.

Similarly, it has been argued that the transfer of offspring from one allomother to another is a "highly orchestrated" act which means that, to some extent, individuals are capable of monitoring the behavior of other caretakers and adjusting their own behavior accordingly (Burkart, Hrdy, & van Schaik, 2009, p. 179). Cronin, Kurian, & Snowdon (2005) suggest that cotton-top tamarins (*Saguinus oedipus*) are capable of understanding the role that their partner plays while engaging in a cooperative task. It seems that the capacity to tolerate, monitor, and help others has aided the advancement of callitrichid social cognition (Burkart, 2009). Indeed, callitrichids seem to have enhanced vocal plasticity (Snowdon, 2001), social tolerance (Burkart, 2015), social learning abilities (Burkart, Kupferberg, Glasauer, & van Schaik, 2012; Caldwell & Whiten, 2004; Dillis, Humle, & Snowdon, 2010; Gunhold, Massen, Schiel, Souto, & Bugnyar, 2014), flexibility in social contexts (Burkart & Heschl, 2007; discussed further p. 15), and cooperative abilities (Burkart, Fehr, Efferson, & van Schaik, 2007).

## 3.4 Study species: the common marmoset (Callithrix jacchus)

Common marmosets (*Callithrix jacchus*), native to Brazil, are small callitrichid monkeys that have been relatively successful in living in various types of forests (coastal, semi-deciduous, savanna, riverine, dry secondary; Ford, Porter, Davis, & Tuttle, 2009). They are capable of invading new habitats and surviving in urban areas by making adjustments to their behaviors and diets (Abreu, De la Fuente, Schiel, & Souto, 2016; Castro & Araújo, 2006); something which has been attributed to their high "ecological and behavioral plasticity" (Rodrigues & Martinez, 2014). Common marmosets are also anatomically adapted for gummivory; their sharp, claw-like nails allow them to extract gum from trees. It has been suggested that this adaptation allows *Callithrix* species to utilize tree exudates as a stable source of food, leading to

home ranges that are smaller than typical sizes for species of other genera (Hubrecht, 1985). Their adaptation for gummivory has also been linked to their apparent "patience" and abilities in delayed gratification (willingness to wait for a larger reward instead of obtaining an immediate small reward; Stevens et al., 2005). Spaulding & Hauser (2005) argue that inhibitory control allows for more thorough exploration and attention to "featural differences" in tools and other stimuli and Adriani et al. (2013, p. 554) claim that common marmosets lack "delay-induced, cognitive impulsivity."

In the social domain, common marmosets are highly social and live in extended family groups ranging from three to 15 individuals (Badihi, 2006). In addition to using various facial expressions (Kemp & Kaplan, 2013), both captive and wild individuals have been observed to use vocalizations during periods of threat, aggression, play, foraging, feeding, and rest (Bezerra & Souto, 2008) and there seem to be different "dialects" among different populations (Zürcher & Burkart, 2017). They have been studied extensively, both in the wild and in captivity, with a range of tasks to measure their social (Burkart & Heschl, 2006, 2007; Burkart et al., 2012; Caldwell & Whiten, 2003, 2004; Gunhold et al., 2014; Voelkl & Huber, 2007) and physical (Bugnyar & Huber, 1997; Cacchione & Burkart, 2012; Halsey, Bezerra, & Souto, 2006; Yamazaki et al., 2011) cognitive abilities. They are also commonly used as test subjects for biomedical and neuroscientific research, as they seem to survive relatively well in captivity (Collins, Wilkinson, Everitt, Robbins, & Roberts, 2000; Dettling et al., 2002; Pryce et al., 2004).

In terms of cooperative breeding, even marmosets with no experience with parental care express high rates of alloparental behaviors; something which may be linked to increased levels of the hormone prolactin (Roberts et al., 2001). Increased prolactin seems to be associated with physical contact with infants and rises as the number of infants being carried in a group increases, rather than being associated with the infant's birth (da Silva Mota, Franci, & De Sousa, 2006). Furthermore, after measuring cortisol levels in non-reproductive males exposed to opened and closed transparent boxes with an infant inside, Barbosa & da Silva Mota (2013) suggest that prior exposure to infants and

experience with caregiving influences the responsiveness of these individuals to sensory cues from newborns through increased cortisol levels.

The hormone oxytocin also seems to mediate caretaking behavior in common marmosets. For instance, in a captive study, Finkenwirth, Martins, Deschner, & Burkart (2016) found that mean oxytocin levels increased significantly in all group members after birth, were highest in female breeders, and were associated with care-taking behaviors like food-sharing. Unfortunately, there are no studies which compare breeders to helpers in terms of physiology and how this may drive differences in cognition or personality.

Overall, common marmosets, like all cooperatively breeding callitrichids, demonstrate high levels of tolerance, prosociality, and cooperation (Burkart, 2009). For example, in a series of experiments Burkart & Heschl (2006, 2007) found that marmosets are capable of geometrical gaze following (tracking the direction and target of gaze) and use this ability to modify behavior. Furthermore, subordinates who had access to two food rewards would consistently retrieve the reward that their dominant partner could not see – displaying at least a basic form of perspective taking (Burkart & Heschl, 2007). This perspective taking capacity also seems to aid common marmosets in cooperation tasks, where they are relatively successful and able to coordinate their behaviors with one another with little competition or monopolization of resource (Werdenich & Huber, 2002). Marmosets' willingness to cooperate does not seem to be linked to concerns for reputation, as Brügger, Kappeler-Schmalzriedt, & Burkart (2018, p. 1) found a "reverse-audience effect" – with individuals being more likely to share food with infants when others were not watching.

In summary, due to practical and theoretical reasons, common marmosets are a good study species for this undertaking.

# 4 – Inhibitory control in common marmosets (*Callithrix jacchus*): investigating the interplay of curiosity, breeding status, and age

## 4.1 Introduction

Inhibitory control, or motor inhibition, can be understood as the ability to prevent prepotent motor responses (Vlamings et al., 2010). In the past decade, research with human and non-human animals has emphasized the importance of inhibitory control for behavioral flexibility, success on problem-solving tasks, and complex cognition more generally (Vlamings et al., 2010). In their influential study, MacLean et al. (2014) tested 36 species of animals on two classic inhibitory control tasks. A reversal learning, A-not-B task, requires individuals to initially retrieve food from one location (A) but then switch to the other (B) when it is moved to a new location. Here, they must inhibit the learned response of reaching for container A, and instead reach for B (MacLean et al., 2014). Similarly, the cylinder task, a form of detour-reaching, requires individuals to retrieve food from a transparent cylinder following initial exposure to an opaque one. Here, they must inhibit the response of reaching directly for the food and instead reach around and into the cylinder (MacLean et al., 2014). MacLean et al. (2014) found that performance on these tasks was best predicted by a species' absolute brain volume and concluded that larger brains underlie behavioral flexibility.

Behavioral flexibility, or an organism's ability to adaptively modify behavior in response to new or changing circumstances and contingencies, has two components: 1) the ability to acquire new strategies and 2) the ability to abandon old strategies (Bonnie et al., 2012; Coppens et al., 2010; Leal & Powell, 2012). Behavioral flexibility is an important concept because it can inform our understanding of innovation, cumulative culture, the evolution of intelligence or "complex cognition" and evolution itself. Furthermore, a better understanding of behavioral flexibility is important for practical reasons, for reintroducing captive animals in to the wild or fostering flexible behaviors in human children. Tests of

inhibition, like the detour reaching task, are frequently used as a proxy for behavioral flexibility (Amici et al., 2008; Manrique, Völter, & Call, 2013). But is this really an accurate measure of such a complex trait; are there other factors that influence inhibition that must be taken in to account when making conclusions about behavioral flexibility?

Recently, Tello-Ramos et al. (2019) claimed that the main mechanism that prevents behavioral flexibility is 'proactive interference'. Proactive interference occurs when previously learned information prevents the encoding of novel information in memory; behaviorally this can be understood as conservatism (Hopper et al., 2011), canalization (Edgell et al., 2009), or functional fixedness (Gruber, 2016). Tello-Ramos et al. (2019) argue that individuals with high (vs. low) behavioral flexibility experience less proactive interference and, consequently, worse memory retention. Furthermore, they claim that forgetting is a mechanism that increases behavioral flexibility - through neurogenesis there is a targeted replacement of old memories that are no longer useful. However, when an individual pays attention to novel stimuli, it is more likely that it will be encoded in memory (Chun & Turk-Browne, 2007). Consequently, it is possible that **curiosity** can prevent proactive interference.

Curiosity can be understood as the desire to discover and learn about the environment and ones' relation to it and is an internally motivated form of information seeking (Kidd & Hayden, 2015). In their study of the neural correlates of epistemic curiosity (curiosity about information), Kang et al. (2009) examined human brain activity while presenting participants with trivia questions. They found that heightened curiosity was associated with increased brain activity in areas related to reward (left PFC, caudate) and memory (left IFG, PHG) - especially when the participants made an incorrect guess, suggesting that higher curiosity aids in the encoding of surprising novel information. Furthermore, questions that purported to induce higher curiosity (self-reported by participants) were recalled correctly at higher rates (than low curiosity questions) by participants who returned a week after the initial session to participate in a behavioral study.

In a similar study using novel visual stimuli rather than information, Jepma et al. (2012) found that heightened perceptual curiosity was associated with increased activity in areas related to reward (caudate) and memory (hippocampus). They describe curiosity as an "aversive condition of increased arousal whose termination is rewarding and facilitates memory" (Jepma et al., 2012, p. 1). Overall, it seems that individuals that are more curious are more likely to encode novel information in memory, echoing the theory (Tello-Ramos et al., 2019) that high curiosity may allow for behavioral flexibility by preventing proactive interference.

In their review of the psychology and neuroscience of curiosity, Kidd & Hayden (2015, p. 450) claim that perceptual curiosity is the "driving force that motivates organisms to seek out novel stimuli." Although it is not discussed as "curiosity" per se, studies of exploratory behavior and reactions to novelty (discussed in relation to neophobia and neophilia) seem to show similar results in non-human animals (Bergman & Kitchen, 2009; Byrne, 2013; Day, Coe, Kendal, & Laland, 2003; but see Wang & Hayden, 2019). Individuals can be so curious to the extent that they are willing to put themselves in danger in order to find out more about novel or interesting stimuli (Byrne, 2013; Nissen, 1930; Pisula, Turlejski, & Charles, 2013). But if curious individuals are strongly motivated to explore or approach novel and interesting stimuli, is it possible that they are more or less likely to inhibit habitual responses than their less curious counterparts? How does this crucial component of behavioral flexibility interact with curiosity - a drive which, theoretically, seems to be intimately related? How is this mediated by other factors such as group size or reproductive status?

### 4.1.1 Hypotheses and predictions

This study will look at an inhibition task (detour reaching) and a curiosity task (extended reactions to novelty) in cooperatively breeding monkeys, common marmosets (*Callithrix jacchus*).

Hypothesis: There is an association between inhibition and curiosity, and factors such as age, sex, breeding status, and group size will influence performance in both domains.

The following predictions were made:

- There is an association between curiosity and inhibition; too little is known to predict whether the association will be positive or negative.
- Younger individuals (but not infants, <5, Rylands, 1993) will perform better than older individuals in the inhibition task (Chao & Knight, 1997; Phillips et al., 2019). This seems to be because executive functions in general decline in older age.
- Because there are no conclusive studies on sex-differences in common marmosets in these domains (but see Day et al., 2003), no effect of sex is expected.
- Helpers will have higher inhibition scores than breeders. This is because helpers are responsible for the coordination of caregiving behaviors and infant transfer, and thus may have to inhibit their primary motor instincts more often than breeding individuals (Burkart et al., 2009). Helpers also engage in higher rates of food sharing than breeders, which requires some form of inhibition (to not consume the food themselves; Burkart & van Schaik, 2010; Martins, Antonio, Finkenwirth, Griesser, & Burkart, 2019; Yamamoto & Box, 2010).
- Individuals from larger groups will have lower inhibition scores than individuals from smaller groups. This may be due to the fact that individuals from larger groups are less likely to inhibit a reach towards food because they face more competition for access to resources than those in smaller groups (Griffin & Guez, 2015; Koski & Burkart, 2015).

## 4.2 Methods

### 4.2.1 Ethics Statement

This study conforms to Durham University's Code of Practice for Research. The project has also been reviewed by the Animal Welfare Ethical Review Board (AWERB) at Durham University and has received full ethical approval (Reference: PSYCH-2018-11-09T11:32:04-ksvb83; see APPENDIX A).

### 4.2.2 Piloting

Prior to testing of the main sample, pilot studies were conducted at Kirkley Hall Zoological Gardens (December 2018 – January 2019) and the Birmingham Wildlife Conservation Park (March 2019) with common marmosets (*Callithrix jacchus;* N=2), emperor tamarins (*Saguinus imperator;* N=2), and golden and golden-headed lion tamarins (*Leontopithecus rosalia, Leontopithecus chrysomelas; N= 7*) in order to ensure that all equipment and apparatuses were suitable for callitrichids.

### 4.2.3 Study sample

As summarized in Table 1, 51 common marmosets (*Callithrix jacchus*) from 17 family groups participated in this study. All participants were captive-born, mother-reared and housed in family groups ranging from two to five individuals (with the exception of one individual, who was temporarily separated) at the Primate Station of the Anthropological Institute and Museum of the University of Zurich, Switzerland. Groups were housed in bark mulch floored enclosures (at least 4 $m^3$) consisting of various structures like tree branches, baskets, boxes for sleeping, and an infrared lamp. The groups also had access to an outdoor enclosure when weather conditions were adequate. Their daily feeding schedule consisted of a vitamin and calcium enriched porridge for breakfast, fresh fruit and vegetables for lunch, a protein snack (egg, nuts, fish, etc.), and gum and mealworms for dinner (late afternoon). Water was

available ad libitum through water dispensers. Some of the subjects had prior experience with cognitive tasks but were chosen for this study because they were not participating in other cognitive studies at the time. All data was collected by SG from May to July of 2019, after an initial two-week period of habituation.

*Table 1 – Participants and their characteristics including their sex (m=male, f=female), breeding status (b=breeder or h=helper; breeders are individuals that are currently capable of breeding and are a part of the breeding pair of their group), age (in months), and the family group that they belong to.*

| Name | Sex | Breeding status | Age (months) | Family group |
|---|---|---|---|---|
| James | m | b | 75 | H2 |
| Manuka | f | b | 50 | H2 |
| Nautilus | m | h | 78 | H3 |
| Nebula | f | h | 78 | H3 |
| Lily | f | b | 84 | H4 |
| Nando | m | b | 73 | H4 |
| Vesta | f | h | 177 | H6 |
| Vito | m | h | 157 | H6 |
| Jaja | f | b | 118 | L1 |
| Jandira | f | h | 53 | L1 |
| Jelly | m | h | 36 | L1 |
| Membo | m | b | 121 | L1 |
| Wasabi | f | h | 30 | L2 |
| Washington | f | b | 70 | L2 |
| Werewolf | m | h | 14 | L2 |
| Wolverine | m | h | 14 | L2 |
| Lancia | f | b | 202 | L4 |
| Lexus | m | b | 191 | L4 |
| Lola | f | h | 75 | L4 |
| Lotus | m | h | 84 | L4 |
| Conan | m | b | 69 | L5 |
| Madame | f | h | 15 | L5 |
| Madita | f | h | 15 | L5 |
| Mulan | f | h | 25 | L5 |
| Lex | m | b | 156 | L6 |
| Nougat | f | h | 51 | L6 |
| Nox | m | h | 36 | L6 |
| Nux | f | h | 36 | L6 |

| | | | | |
|---|---|---|---|---|
| Garetta | f | b | 121 | L7 |
| Nuno | m | b | 73 | L7 |
| Tabor | m | b | 128 | L8 |
| Wisconsin | f | b | 70 | L8 |
| Wombat | m | h | 30 | M1 |
| Jamaica | f | h | 44 | R2 |
| Jambi | f | h | 44 | R2 |
| Jupie | f | h | 118 | R2 |
| Marvin | m | b | 148 | R2 |
| John | m | b | 148 | R3 |
| Merkur | m | h | 84 | R3 |
| Mina | f | b | 156 | R3 |
| Mojita | f | h | 50 | R3 |
| Narnia | f | h | 55 | R6 |
| Nirvana | f | h | 55 | R6 |
| Tamino | m | b | 143 | R6 |
| Lea | f | b | 143 | R7 |
| Lima | f | h | 53 | R7 |
| Lynx | m | h | 7 | R7 |
| Craken | m | b | 69 | R8 |
| Ginger | f | h | 14 | R8 |
| Grappa | f | b | 52 | R8 |
| Guapa | f | h | 14 | R8 |

### 4.2.4 Curiosity panel: Apparatus and procedure

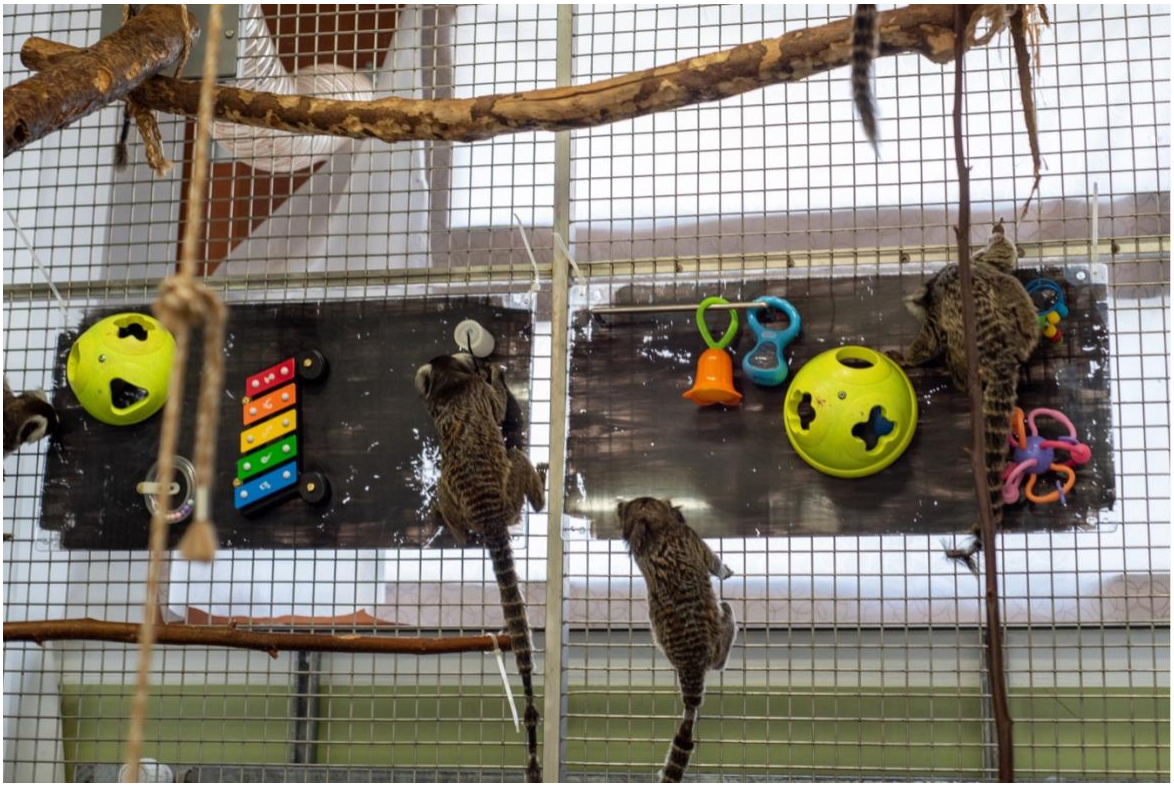


*Figure 2 - Photo depicting curiosity panels provided to common marmosets; with plastic toys, installed in an enclosure at the main study site. From left to right the objects, as discussed in the ethogram below (Table 2) are: yellow globe one, plastic ring, xylophone, film canister, orange flower, blue toy, yellow globe two, abacus toy (top), and soft plastic toy (bottom).*

The curiosity task was administered through two "curiosity" panels consisting of two plexiglass panels (70 x 30 cm) with various novel objects that the individuals had no prior experience with (Figure 2). These were designed with Damerius, Graber, Willems, & van Schaik's (2017) study on orangutan curiosity in mind, where they suggest that curiosity can be behaviorally measured by assessing positive reactions to novelty and exploration levels. The panel included six plastic toys in addition to an abacus-like toy, and a plastic xylophone made for human infants, and a plastic film canister that could be opened and closed (with nothing inside). The panel was fixed to the mesh wall with zip-ties within the group's home enclosure at a height of four feet above the ground, as common marmosets are arboreal and more comfortable the higher above ground they are.

Testing was restricted to 8:30 - 11:00, within three hours of the morning feed. Video recording and live narrated observations based on the ethogram (Table 2) were collected by SG for 30 minutes per day (as in Day et al., 2003) using a GoPro Hero 5, for five days for a total of 150 minutes of observation for each group.

### 4.2.5 Detour reaching Task: Apparatus and procedure

*Figure 3 - Photo depicting detour reaching shelf installed against small cage used to separate individuals at main study site.*

The detour reaching task comprised of a plexiglass shelf (inspired by Wallis, Dias, Robbins, & Roberts, 2001) that was fitted to the outside of each enclosure. The shelf consisted of a transparent plexiglass occluder in the center of a window within the shelf, allowing the animals to reach on to the shelf from either side of the occluder to obtain the food reward (Figure 3).

For testing, individuals were separated from their groups within their home enclosures. Small cages (75 x 40 x 40 cm) were installed against the mesh from the inside of the enclosures one week prior to the start of testing; the individuals could freely enter and exit the cage. All individuals went through a five-day habituation period, where they were rewarded for being alone in the cage with 1/12th of a grape. After an initial reward for entering the cage, individuals were rewarded every 10 seconds the first

day, every 20 seconds the second day, every 30 seconds the third day, every 45 seconds the fourth day, and every minute on the final day until they received a total of five rewards. For the final three days of habituation, the apparatus was also installed against the mesh to give them time to explore and familiarize themselves with it (as pilot studies revealed that some individuals had extreme negative reactions to the apparatus on first presentation). Individuals that displayed frequent pilo-erections, urination, and mobbing behavior as well as individuals that spent more than 30% of the time attempting to leave the cage were identified as unsuitable for testing. However, this should not introduce a confound to the study as Schubiger, Wüstholz, Wunder, & Burkart (2015) found that emotional reactivity towards experimenters within this population impacted participation but not levels of success on cognitive tasks.

All testing was conducted a minimum of 1.5 hours after the afternoon feed. The food reward was always 1/12th of a grape. Once the individual voluntarily entered the cage, the door was closed and the session began. In each trial, the food item was placed on the shelf and behind the plexi-glass barrier. To succeed, the individual had to inhibit the predominant motor response of reaching directly for the food, and instead reach around the barrier in order to retrieve the reward. The individual's first attempt was noted as correct (retrieving the reward) or incorrect (contact of hand with the plexiglass occluder). As in Schubiger et al. (2016), the apparatus remained baited for up to two minutes after the initial incorrect attempt, giving participants the opportunity to continue reaching. If the individual retrieved the reward within two minutes, it was noted as correct after initial failures. If not, the reward was removed after two minutes and the next trial began.

Each individual went through five testing sessions, of 12 trials each, on five consecutive days. For each session the reward was placed in each position (right, left, or middle of the shelf behind the occluder) four times. The order of grape positions was randomized with the restrictions that 1) the first trial of the first session was never in the middle position, 2) the same position did not occur for more

than two consecutive trials, and 3) there were a maximum of two sets of consecutively repeating positions within the 12 trials.

## 4.2. 6 Ethogram and coding of curiosity footage

All curiosity task videos were coded by SG using Mangold Interact behavioral video coding software using a dedicated ethogram, developed for this study (Table 2) based on criteria used by Damerius et al. (2017) and Santillán-Doherty, Muñóz-Delgado, Arenas, Márquez, & Cortés (2006).

*Table 2 - Ethogram for coding curiosity panel footage*

**Whenever individuals were within one body length of the panel, they were coded as engaging in one of two sets of orientation behaviors:**

- **Attention/smelling (A/S):** visual or olfactory attention where the face must be oriented towards the panel within an angle of 45 degrees (to the left or right) of head rotation; can be accompanied by physical contact in the form of grazing or for use as support (part or all of animal's weight is being carried by the panel); can be toward the panel or one of the objects on the panel.
- **Manipulating (M):** physical contact with an object on the panel with hands, feet, or mouth that is "directed towards the unique characteristics of an object" and alters the object in a way that changes it from its original state (Lamon, Neumann, & Kuberbuhler, 2018); can be accompanied by attention/smelling; can be toward one of the objects on the panel.

**An event began when an individual was within one body length of the panel and A/S or M began. The end of the bout was noted when 1) the individual disengaged from the panel or objects (face no longer oriented within an angle of 45 degrees for A/S and end of physical contact for M) for more than 2 seconds, or 2) when the individual engaged with a different object or the panel.**

**Further notes for manipulation criteria for each object (Figure 2) included:**

- Yellow globe 1: object inside is moved from original position
- Plastic ring: ring is either rotated in place or moved (left-right) from original position
- Xylophone: physical contact with the xylophone with hands, feet, or mouth directed towards the base, pegs, or bars of the xylophone that is an *attempt* to alter or move these pieces; attempts include vigorous movement which would cause the xylophone parts to move if it was possible
- Film canister: physical contact with the film canister with hands or mouth directed towards the string and/or cover of the canister that is an attempt to alter or move these pieces; attempts include vigorous movement which could cause the film canister to open or the string to detach if the animal was stronger
- Orange flower: moved from original position on bar (sliding) or rattled in place
- Blue toy: moved from original position on bar (sliding) or rattled in place
- Yellow globe 2: object inside is moved from original position
- Abacus toy: beads are rotated in place or moved (sliding) from their original position
- Soft plastic toy: small pink attachments are either rotated in place or moved (sliding) from their original position

### 4.2.7 Data analysis and statistics

All statistical analyses were conducted in R 3.5.1 using RStudio 1.1.456.

#### *4.2.7.1 Principal Component Analysis: Curiosity score*

In order to look at the association between curiosity and inhibition scores, first a "curiosity measure" was produced that reflected the different components of the data collected on the curiosity panel. Seven variables were extracted from the video: latency to contact, A/S duration, M duration, A/S frequency, M frequency, A/S diversity, and M diversity. Initially, latency to first contact with the panel as well as the duration and frequency of 1) attention/smelling (A/S) and 2) manipulation (M) for each object and individual as well as for each of the five sessions was extracted (18 variables). The durations of A/S or M by object were calculated by dividing the total time of A/S and M for each object by the total time of the observation session (30 min). On the other hand, the frequency of A/S or M by object was calculated by dividing the number of interactions with the respective object by the total amount of time the individual spent in close proximity to the panel. This "frequency of interactions per minute" captured how fast the animals were engaging and disengaging with the respective objects. Behavioral measures were not based on the individual scores by object but rather on the total amount of time spent with the panel/objects for each session. Additionally, the percentage of the objects that each individual interacted with for each of the sessions was also calculated in order to create a "diversity of interaction score" for both A/S and M.

The resulting seven variables were all continuous, linear relationships exist between them, Bartlett's test was significant ($\chi2(21)=1606.485$, $p < .0001$), the Kaiser-Meyer-Olkin factor was greater than .5 (MSA = .75), and there were no significant outliers – meaning the data was suitable for a PCA. A PCA was run using these seven variables (total durations, not parsed by object; see Table 3 for correlation matrix). The PCA was rotated to increase the "interpretability" of the factors, so that positive scores reflected "higher" curiosity. Parallel analysis was performed to decide which factors to retain: 10,000 random data sets were generated (with equal sample size and dimensionality – rows and columns - as the actual data) and components with Eigenvalues greater than the 95% quantile value

were extracted; this means that only components that explain more variance than a randomly generated dataset were retained.

*Table 3 - Correlation matrix of initial PCA*

| | Latency to contact | A/S duration | M duration | A/S frequency | M frequency | A/S diversity | M diversity |
|---|---|---|---|---|---|---|---|
| Latency to contact | 1.00 | -0.40 | -0.18 | -0.40 | -0.25 | -0.48 | -0.29 |
| A/S duration | -0.40 | 1.00 | 0.61 | -0.20 | 0.33 | 0.82 | 0.65 |
| M duration | -0.18 | 0.61 | 1.00 | -0.29 | 0.59 | 0.57 | 0.72 |
| A/S frequency | -0.40 | -0.20 | -0.29 | 1.00 | -0.18 | -0.08 | -0.25 |
| M frequency | -0.25 | 0.33 | 0.59 | -0.18 | 1.00 | 0.45 | 0.76 |
| A/S diversity | -0.48 | 0.82 | 0.57 | -0.08 | 0.45 | 1.00 | 0.68 |
| M diversity | -0.29 | 0.65 | 0.72 | -0.25 | 0.76 | 0.68 | 1.00 |

The first factor loaded highly on the two duration measures, the M frequency, and the two diversity measures (APPENDIX B). However, latency to first contact and A/S frequency loaded highly on the second component, with the two factors being negatively correlated. This means that individuals with longer latency to approach the panel also interacted with the panel at a quicker pace once they approached it (captured by A/S frequency). Because latency and A/S frequency seem to measure a different "axis" of the interaction with the panel, "exploration speed" or "social influence" per se – rather than "curiosity," they were removed from the PCA and the PCA was repeated with the remaining factors.

Parallel analysis was again conducted to determine which components of the final PCA should be retained. Based on this (see APPENDIX C), the first component was retained as a "curiosity score" for each individual for each session (Table 4). The factor was multiplied by -1 to make the scores more intuitive, with higher, positive scores denoting more curious individuals.

*Table 4 - Final PCA summary*

| **Behavior** | **Factor loading** |
|---|---|
| | *PC1* |
| % variance | 69.77% |
| Standard deviation | 1.869 |
| A/S duration | 0.94 |
| M duration | 0.52 |
| M frequency | 0.11 |
| A/S diversity | 0.88 |
| M diversity | 0.52 |

Finally, the five curiosity scores for each of the five sessions were averaged, producing a single summary "curiosity score" for each individual. This was done because the score is supposed to be a measure of curiosity rather than "neophobia," which may be captured by the first session only.

#### *4.2.7.2 Inhibition score*

The percentage of total trials completed with a successful, first-try detour reach in the detour-reaching task were calculated for each individual. To ensure that hand preference was not skewing the results (Cameron & Rogers, 1999), a score for each of the grape positions (right, middle, left) was extracted from the data and chi-square tests were run for each individual to compare the performance between lateral trials (right and left). This revealed that nine out of N = 51 individuals (17.6% of the sample) had a significant side-bias (see APPENDIX D), which is not more than what would be expected by chance even with no side bias when using the $p < .05$ criteria across multiple tests. Moreover, no significant difference was found, in terms of overall task success, between individuals with a side bias and individuals without (t-test, N=51, $t = 1.045$, $p = .301$). Accordingly, the percentage of total trials completed successfully was retained as an "inhibition score" for each individual.

#### *4.2.7.3 Fitting the model*

To analyze whether an individual's inhibition score (the dependent variable) was associated with curiosity, sex (male or female), breeding status (helper or breeder), age (in months, 7-202), and group size (1-5), linear mixed-models (LMM) were created in R using the function "lmrob" from the package "robustbase." Visual checks and a Shapiro-wilks normality test revealed that the inhibition score was normally distributed (p = .238). In all the models, the subject nested in the family group was set as a random factor.

In the final model (Table 5), curiosity score and breeding status, sex, age, and group size were included as predictors, as well as the three-way interaction between age, status, and curiosity score. This interaction was included based on initial exploration of the curiosity score (Figure 5); adding the interaction significantly improved the fit of the model (checked using "deviance" anova; f(2) = 11.44, p < .01). The individual nested in family group was included as a random effect. The model was checked using several model diagnostics (including VIFs, inspection of residuals, dffits), none were indicative of any deviations from the assumptions of normality and homogeneity of residuals (APPENDIX E).

*Table 5 - Final model*

| Dependent variable | Fixed factor/effect | Estimate | Standard Error | t-value | p-value | 95% Confidence Intervals | |
|---|---|---|---|---|---|---|---|
| Inhibition score | Intercept | 72.898 | 12.101 | 6.024 | <.001 | 49.180 | 96.615 |
| | Curiosity score | -11.363 | 4.248 | -2.675 | .011 | -19.690 | -3.037 |
| | Sex | 3.511 | 6.094 | 0.576 | .568 | -8.434 | 15.456 |
| | Breeding status | 5.066 | 8.239 | 0.615 | .542 | -11.082 | 21.215 |
| | Age | -0.187 | 0.095 | -1.966 | .056 | -0.374 | -0.001 |
| | Group size | -5.594 | 2.547 | -2.196 | .034 | -10.586 | -0.602 |
| | Age*status*curiosity (breeder) | 0.143 | 0.060 | 2.359 | .023 | 0.024 | 0.262 |
| | Age*status*curiosity (helper) | 0.193 | 0.117 | 1.655 | .105 | -0.036 | 0.422 |

# 4.3 Results

## 4.3.1 Initial analysis of curiosity score

Initially, the curiosity score was inspected individually and in relation to age, sex, breeder status, and group size. In terms of age, curiosity score decreased as individuals get older (Figure 4; linear model (lm), curiosity score ~ age, t=-3.408, p = .001).

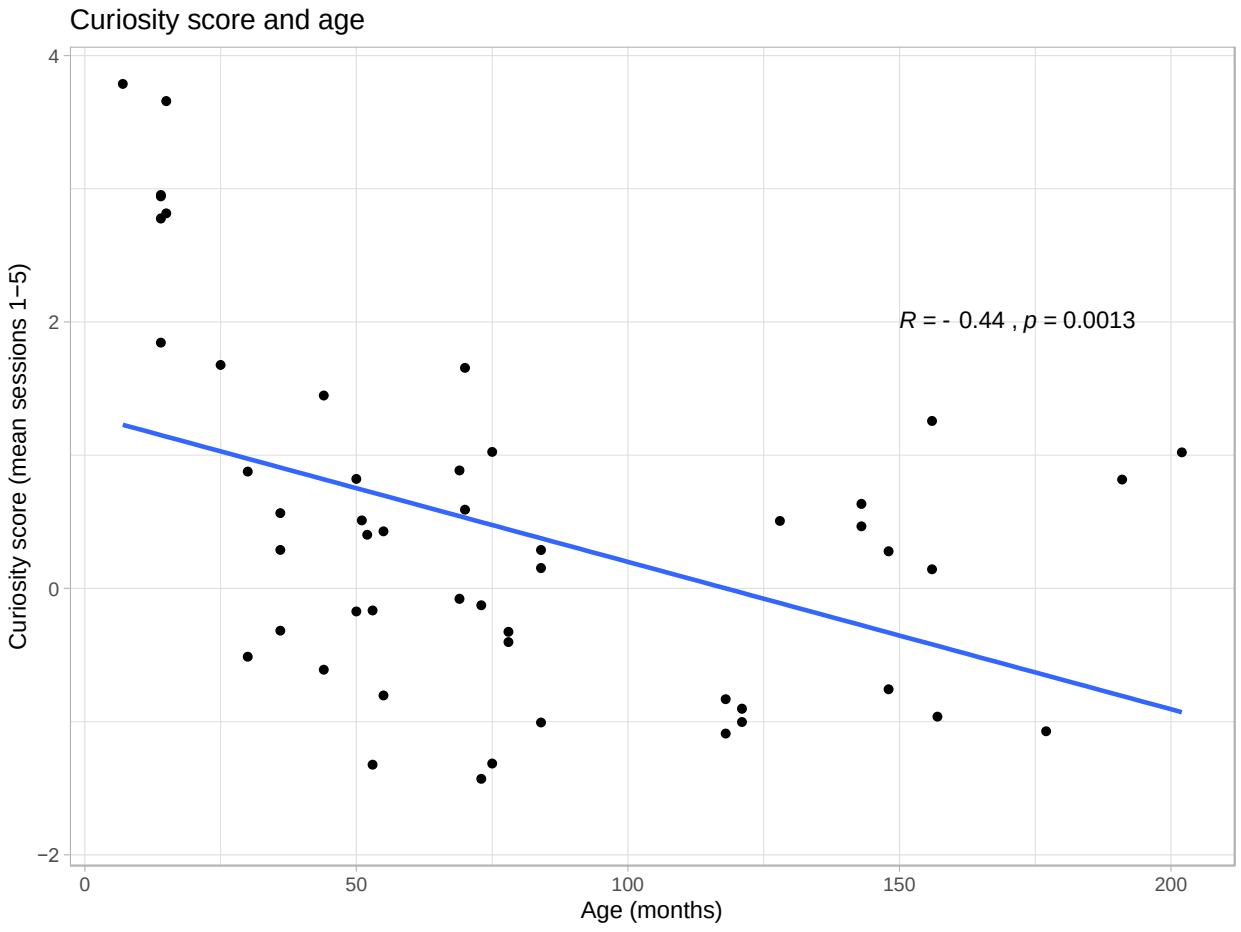



*Figure 4 - Curiosity score by age in months. Each point indicates the curiosity score (mean of sessions 1-5) for each individual with higher scores denoting higher curiosity. The blue line was fitted using Pearson's correlation; grey areas represent standard error.*

A pattern emerges, again, when the relationship between curiosity score and age is looked at for breeders and helpers separately (Table 6). Although breeders' curiosity stays relatively stable with age, helpers seem to become less curious as they age (Figure 5).

*Table 6 - Linear model looking at effect of age and breeding status (Curiosity score ~ age + breeding status + age*breeding status)*

| Dependent variable | Fixed factor/effect | Estimate | Standard Error | t-value | p-value |
|---|---|---|---|---|---|
| Curiosity score | Intercept | -0.522 | 0.594 | -0.879 | .384 |
| | Age | 0.005 | 0.005 | 1.009 | .318 |
| | Breeding status | 2.570 | 0.672 | 1.826 | <.001 |
| | Breeding status*age (helper) | -0.030 | 0.007 | -4.341 | <.001 |

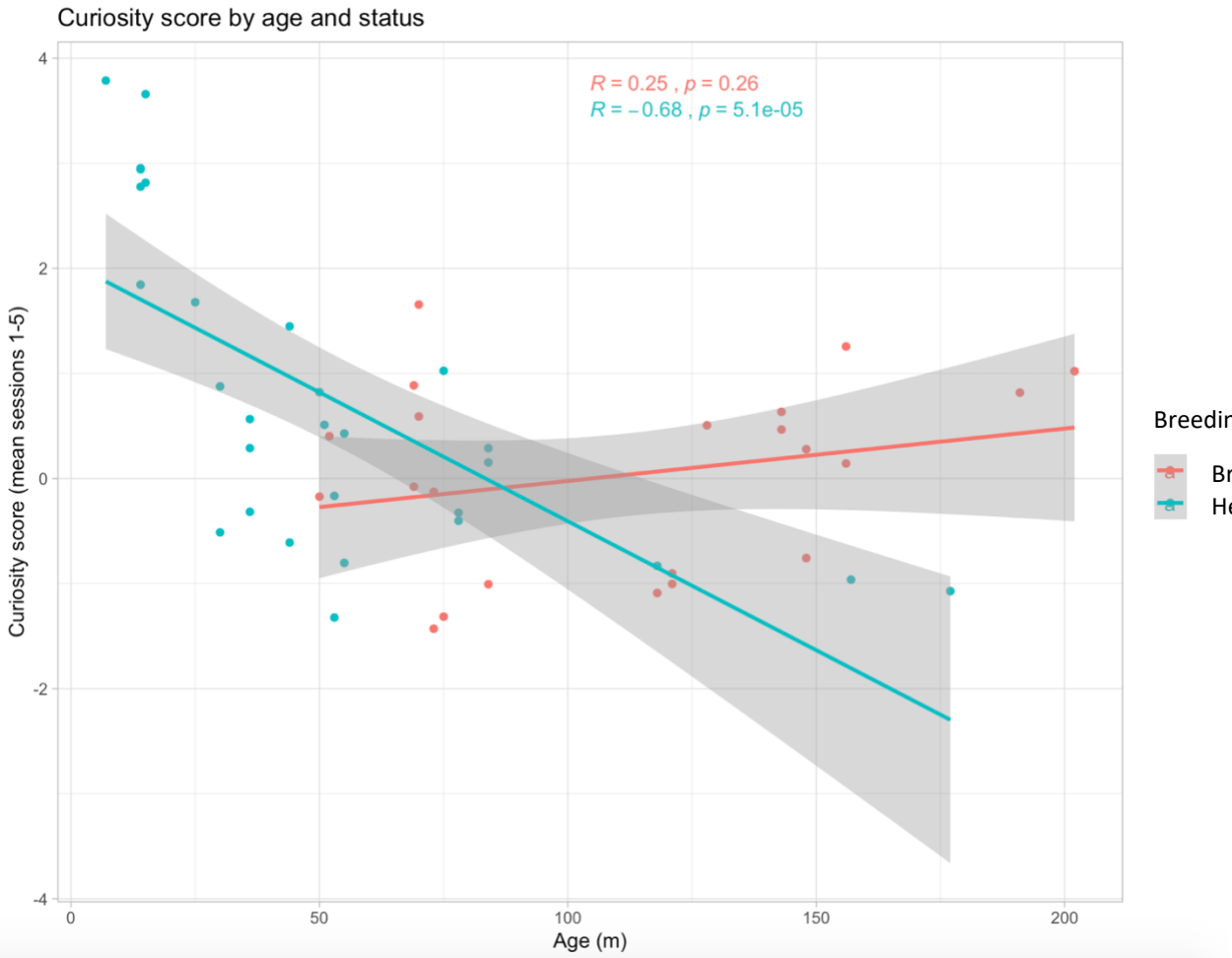



*Figure 5 - Curiosity score by age (in months) and breeding status (breeder or helper); Each point indicates the curiosity score (mean of sessions 1-5) for each individual with higher scores denoting higher curiosity. Lines were fitted using Pearson's correlation (corresponding p-values provided top center); grey areas represent standard error.*

It also may be that breeding status has an effect on curiosity score independently of age, with helpers scoring higher than breeders (ANCOVA, curiosity score ~ status + age, status: f(1)=4.341, p = .042; age: f(1)=7.090, p = . 011). Sex, on the other hand, seems to have little or no effect on curiosity score; t-test, t(44.679)=0.550, p = .585 (Figure 6).

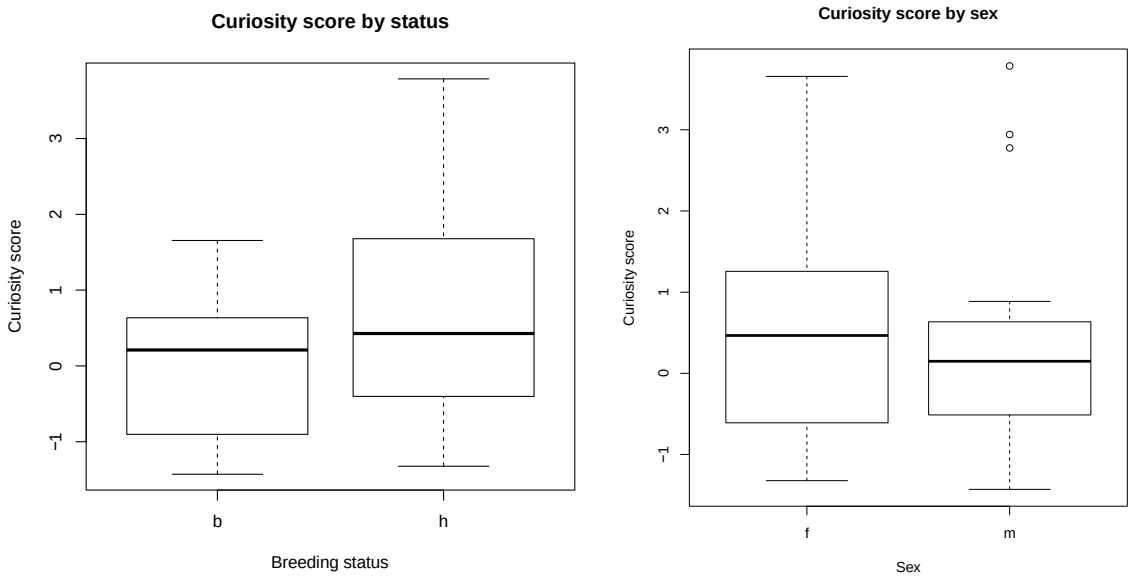



*Figure 6 - Boxplots of curiosity score by breeding status and sex; showing the minimum, first quartile, median, third quartile and maximum curiosity score for breeders and helpers, and females and males respectively.*

Finally, group size also seems to be important for curiosity score, with individuals from larger groups obtaining higher curiosity scores on average (lm, curiosity score ~ group size, t=2.603, p = .012; Figure 6).

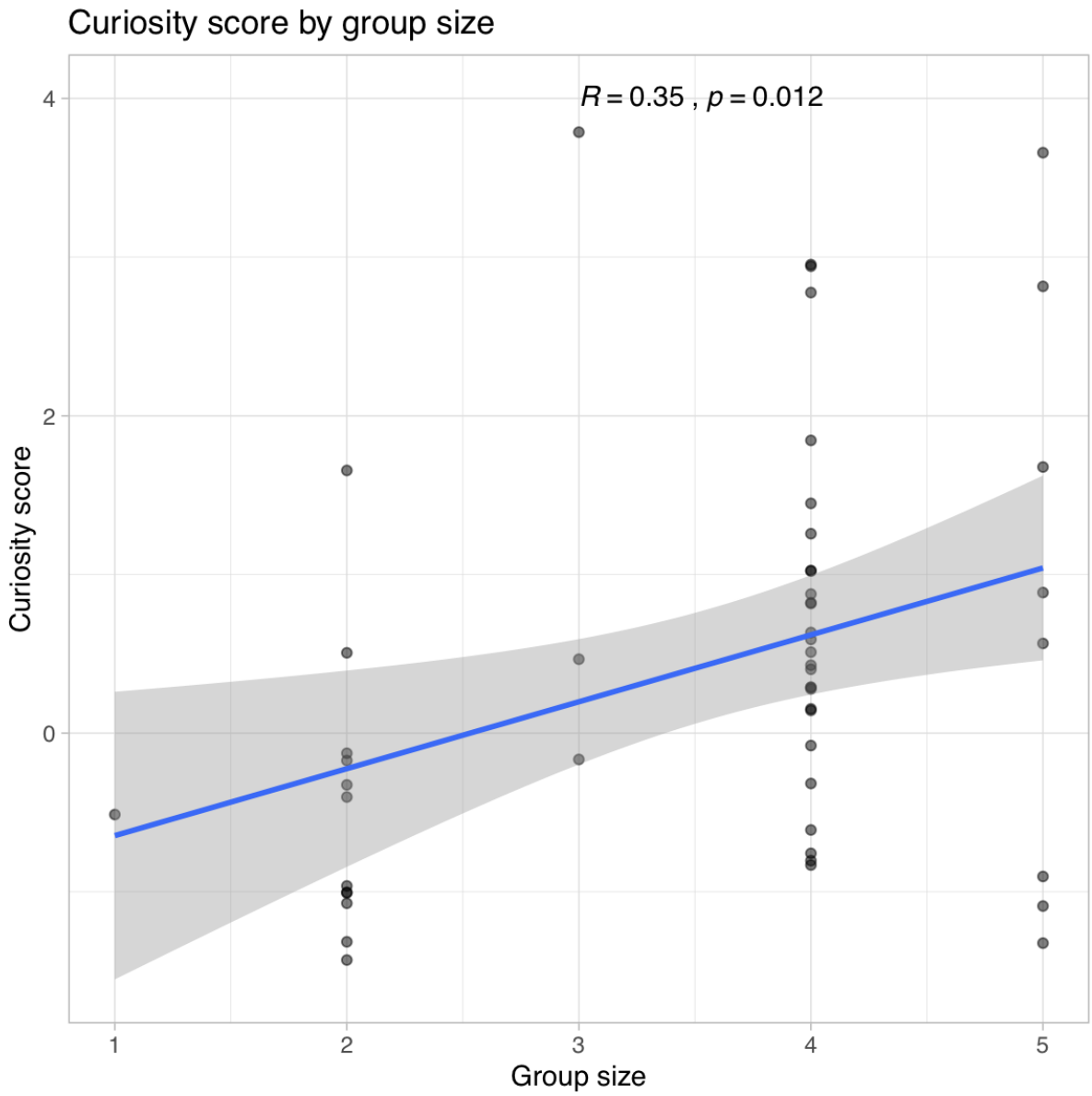



*Figure 7 - Curiosity score by group size; Each point indicates the curiosity score (mean of sessions 1-5) for each individual with higher scores denoting higher curiosity. The blue line was fitted using Pearson's correlation (p-values provided top center); grey areas represent standard error.*

### 4.3.2 Inhibition score: results from final model

The predicted values of the inhibition score based on the final model (Table 5) are presented for group size (Figure 8), where larger groups perform more poorly on the inhibition task, and for the interaction

between age, breeding status, and curiosity score (Figure 9), with differences emerging between highly curious helpers (who have relatively higher inhibition scores) and breeders – especially at older ages.

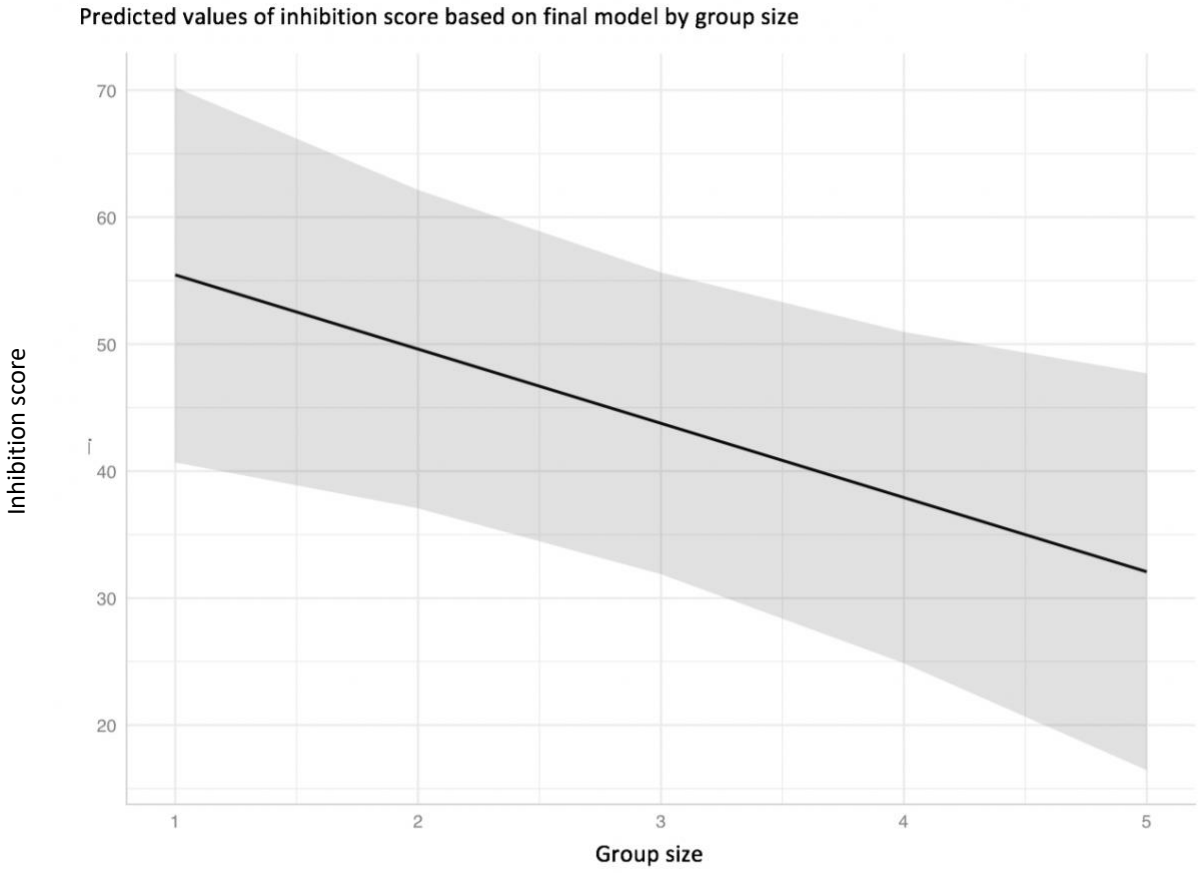



*Figure 8 - Predicted values (estimated from final model) of inhibition score based on the size of the group; grey areas denote 95% confidence intervals. Individuals from smaller groups outperform individuals from larger groups.*

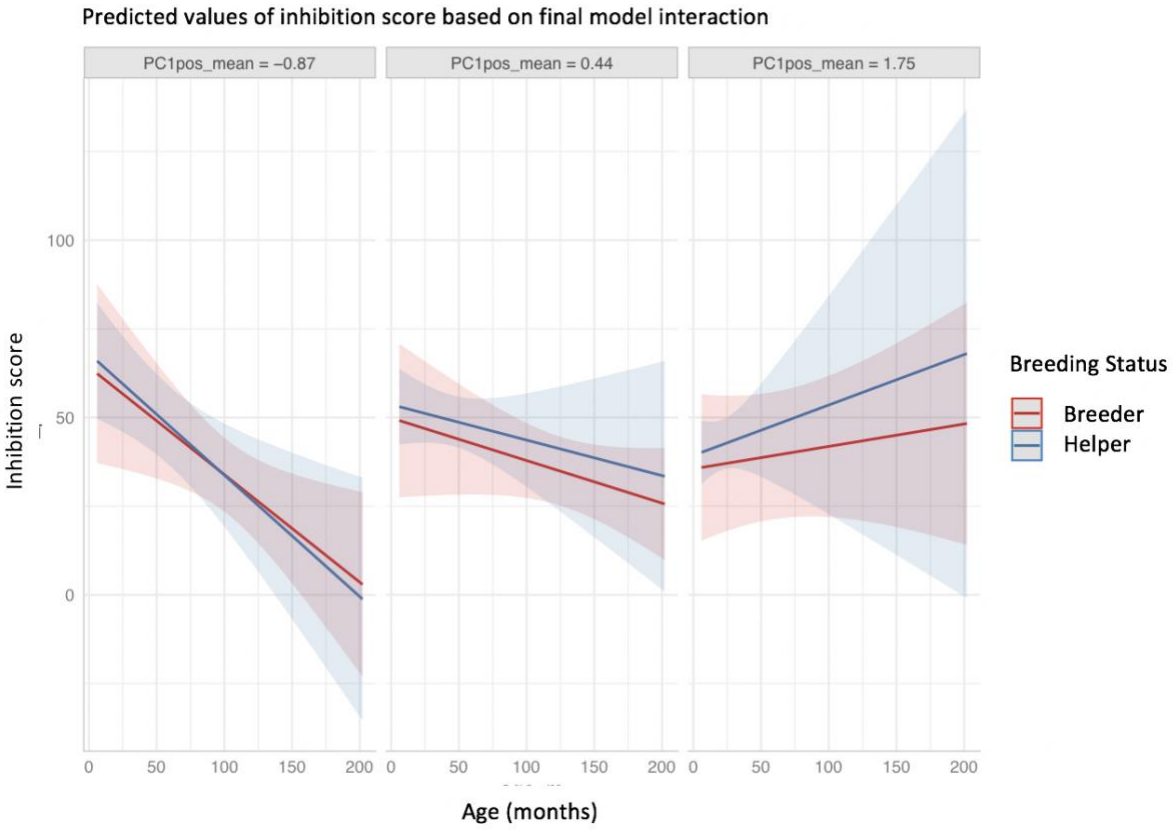



*Figure 9 - Predicted values (estimated from final model) of inhibition based on interaction (age*status*curiosity) for relatively low, medium, and high curiosity; shaded areas denote 95% confidence intervals.*

## 4.4 Discussion

In research on animal behavior, inhibitory control has been used as a proxy for behavioral flexibility and even intelligence (Mikhalevich et al., 2017). The aim of this study was to investigate whether curiosity and other related characteristics predict performance on one measure of inhibitory control, the detour-reaching task (Kabadayi et al., 2018), in a cooperatively breeding monkey species, the common marmoset. The resulting model reveals that group size as well as an interaction between

curiosity, age and breeding status predict inhibitory control. There was no effect of sex. Overall, these results highlight the importance of considering individual physical, cognitive, and social characteristics when making conclusions about complex concepts like behavioral flexibility.

As predicted, there was a significant negative effect of group size on inhibition scores (Figure 8) i.e., individuals from larger groups were less able to inhibit prepotent responses. As Koski & Burkart (2015) discuss, common marmosets display within-group similarities in personality traits that are not driven by genetic relatedness. The result may also be explained by enhanced feeding competition i.e. individuals in larger groups may experience "competition" for food resources; if they wait or inhibit the urge to take food, it may not be there when they return. On the other hand, individuals from smaller groups are less likely to face this risk (Price & Stoinski, 2007).

Results reveal a significant interaction between age, status, and curiosity score (Figure 9). While inhibition seems to have a negative relationship with age in individuals that are not highly curious, the opposite is true for individuals that have high levels of curiosity. Furthermore, this positive relationship seems to be stronger for helpers than for breeders. The finding that age generally has a negative relationship with inhibition in marmosets is not surprising, as this has been well documented in many species, including humans (Chao & Knight, 1997; Sweeney, Rosano, Berman, & Luna, 2001; Tapp et al., 2003; West & Alain, 2000). However, what is more telling is the patterns observed for individuals with high curiosity. It seems that, in some way, high curiosity not only "protects" individuals from declining motor inhibition brought on by aging but is also associated with enhanced motor inhibition. Although not conducted with common marmosets, Damerius et al.'s (2017) study on orangutans can shed some light on these results. They tested captive orangutans on five novelty response and exploration tasks and five problem-solving tasks, one of which was detour reaching. For all of the problem-solving tasks, the likelihood that individuals would be successful had a positive relationship with curiosity levels, and this effect was strongest for the detour-reaching task (Damerius et al., 2017, p. 63). It is possible that

curiosity aids in tasks that require trial and error learning or simply that high curiosity allows individuals to perform successfully because they are more engaged with the task more generally.

The study indicates an interaction between breeding status, age, and curiosity with helpers experiencing a much sharper improvement in inhibition scores with age; these factors were all predicted to have some influence. Two possible explanations exist. On one hand, being responsible for carrying, caring for, and sharing food with infants may require enhanced inhibition as helpers will need to inhibit their own motivations in order to ensure infant survival (share food; Yamamoto & Box, 1997). Furthermore, breeders have priority of access to food (Epple, 1970; Tardif & Richter, 1981), possibly forcing helpers to inhibit their impulse to retrieve food more often. It may be that motor inhibition skills greatly benefit when these experiences are coupled with high curiosity.

On the other hand, it is possible that this result reflects the effects of captivity. In their study of infant survival rates in captive marmosets Rothe, Koenig, & Darms (1993) found that survival rate was not correlated with number of group members or number of adult members – survival rate remained relatively constant (~80%) across groups. So, it is possible that captive helpers do not play a large role in ensuring the survival of offspring, perhaps giving them extra time for exploration throughout the lifetime. Helpers with extra time that are curious may explore more frequently or are simply more attentive to their surroundings, and the detour-reaching task, which leads to higher scores. Helpers with extra time that are not curious, however, may have little exploratory motivation, leading to lower inhibition scores.

While this study provides novel insights, it comes with certain limitations which might constrain the conclusions that can thus far be made. Most notably, only one inhibition task was used; utilizing multiple tests of inhibitory control could further strengthen these results. Furthermore, inhibitory control is only one component of behavioral flexibility (Audet & Lefebvre, 2017). Studies examining the relationship between curiosity and other components (e.g. reversal learning, set-shifting) are necessary

to gain a more accurate understanding of how behavioral flexibility and curiosity are related. All subjects were housed in the same location in captivity; a more diverse sample could help to obtain a clearer picture of these phenomena. Studies with wild samples are also necessary to reinforce our understanding. Finally, further studies are needed to validate this measure of curiosity and refine it in order to ensure that it is an accurate measure.

## 4.5 Conclusion

The complexity of concepts like behavioral flexibility is highlighted by the fact that even a single component cannot be accurately understood without taking in to account various other individual characteristics and propensities. This study demonstrates that motor inhibition is impacted by group size and age, breeding status, and curiosity level in a very intricate way in a cooperatively breeding monkey species. Not only is this important to our understanding of behavioral flexibility more generally, but also for biomedical research and studies on aging and motor inhibition which do not account for levels of curiosity or breeder/helper status (Murai et al., 2013; Okano, Hikishima, Iriki, & Sasaki, 2012; Spinelli et al., 2005).

# 5 – General Conclusion

Behavioral flexibility is a complex, emergent property that has many components and is influenced by numerous characteristics. As demonstrated by my study, several factors impact just a single component of flexibility in complex and dynamic ways. To ensure that our understanding of behavioral flexibility, and other concepts like curiosity and cooperative breeding, is empirically accurate, consistent definitions and testing paradigms are required before making conclusions. Below, I propose a broad definition and guide that can be used in future studies of behavioral flexibility.

## 5.1 Theoretical contribution and future directions

Building upon and extending insights from previous work, my study provides potential to build a new definition of behavioral flexibility: Behavioral flexibility refers to an organism's ability to adaptively modify behavior in response to new or changing circumstances and contingencies; this refers to changes not only in a behavior, but also in the rules that determine the performance of that behavior. This requires 1) the ability to acquire new strategies and 2) the ability to abandon old strategies; which themselves have underlying components that vary in differing circumstances. Essentially, there is no direct route to testing behavioral flexibility as it seems to be an "emergent property" dependent on varying skills and characteristics that also vary among different individuals and contexts (Griffin, 2016).

In order to understand how behavioral flexibility emerges, it is important to identify the factors that foster or impede it in different situations and environments. By explicitly stating: 1) the components of behavioral flexibility that are being tested, 2) the contextual factors that may have an effect, and 3) the relevant characteristics of the individual and species - future studies can work to tease out the numerous aspects that must be considered (see Table 7).

Future studies could also directly investigate the link between experimental tests of behavioral flexibility and observations of behavioral flexibility in the wild (Pritchard, Hurly, Tello-Ramos, & Healy, 2016). Does performance on a reversal-learning or detour task have any relationship to the same individual's flexibility in foraging behavior in a naturalistic setting? Are actual rates of exploratory behavior in the wild related to performance on an experimental puzzle boxes or extractive foraging tasks? Does captivity have differing effects on various measures of behavioral flexibility? These are all questions that could potentially be answered by combining and comparing observational and experimental methods.

*Table 7 - Behavioral flexibility suggested guidelines for future studies based on literature review and study result.*

| **It would be beneficial if future studies indicated…** |
|---|
| **(i) which components of behavioral flexibility are being tested:**<br>• *Attention*<br>• *Inhibition*<br>• *Divergent thinking*<br>• *Physical cognition*<br>• *Discrimination learning*<br>• *Categorization/concept learning*<br>• *Neophilia/curiosity*<br>• *Neophobia* |
| **(ii) contextual factors that may impact the individuals in the particular study:**<br>• *Prior knowledge and experience*<br>• *Stress*<br>• *Presence of conspecifics*<br>• *Exposure to danger*<br>• *Food availability/dietary constraints*<br>• *Captivity*<br>• *Reproductive status*<br>• *Novelty and complexity* |
| **(iii) individual and species characteristics that may be influential:** |

- *Age*
- *Sex*
- *Social status*
- *Feeding ecology*
- *Social dynamics/complexity*
- *Motor diversity/complexity*
- *Energetic state/energy expenditure*
- *Brain size*
- *Developmental constraints*

This thesis as a whole has highlighted the importance of having precise definitions and coherent conceptual frameworks when investigating complex concepts more generally. It is my hope that my review, study, and resultant recommendations for studies of behavioral flexibility will encourage 1) studies that experimentally test animal's propensities for the distinct components of behavioral flexibility, 2) identification of factors that influence the likelihood of the components of behavioral flexibility through observation, which will make way for 3) the creation of a comprehensive model of behavioral flexibility that can be used to predict, measure, and understand the propensity for behavioral flexibility in animals. This may further progress towards 4) uncovering the relevant neural mechanisms and brain regions involved in behavioral flexibility, and 5) informing our understanding of innovation, cumulative culture, and the evolution of cognitive abilities more generally. The resulting model may additionally 6) inform programs that aim to increase behavioral flexibility in captive animals, especially those that are being prepared to be reintroduced to the wild.

# Appendices

## APPENDIX A – Ethical approval

Dear Samin,

The following project has received ethical approval:

Project Title: *Behavioral flexibility and curiosity in callitrichids;*
Start Date: *22 December 2018*;
End Date: *30 April 2019;*
Reference: *PSYCH-2018-11-09T11:32:04-ksvb83*
Date of ethical approval: *23 January 2019*.

# APPENDIX B – Factor loadings for initial PCA

| **Behavior** | **Factor loading** | |
|---|---|---|
| | *PC1* | *PC2* |
| % variance | 71% | *29%* |
| Standard deviation | 3.71 | *1.49* |
| Latency to contact | -0.39 | -0.81 |
| A/S duration | 0.82 | 0.17 |
| M duration | 0.84 | -0.15 |
| A/S frequency | -0.31 | 0.83 |
| M frequency | 0.74 | -0.08 |
| A/S diversity | 0.84 | 0.29 |
| M diversity | 0.91 | -0.05 |

# APPENDIX C – Parallel analysis

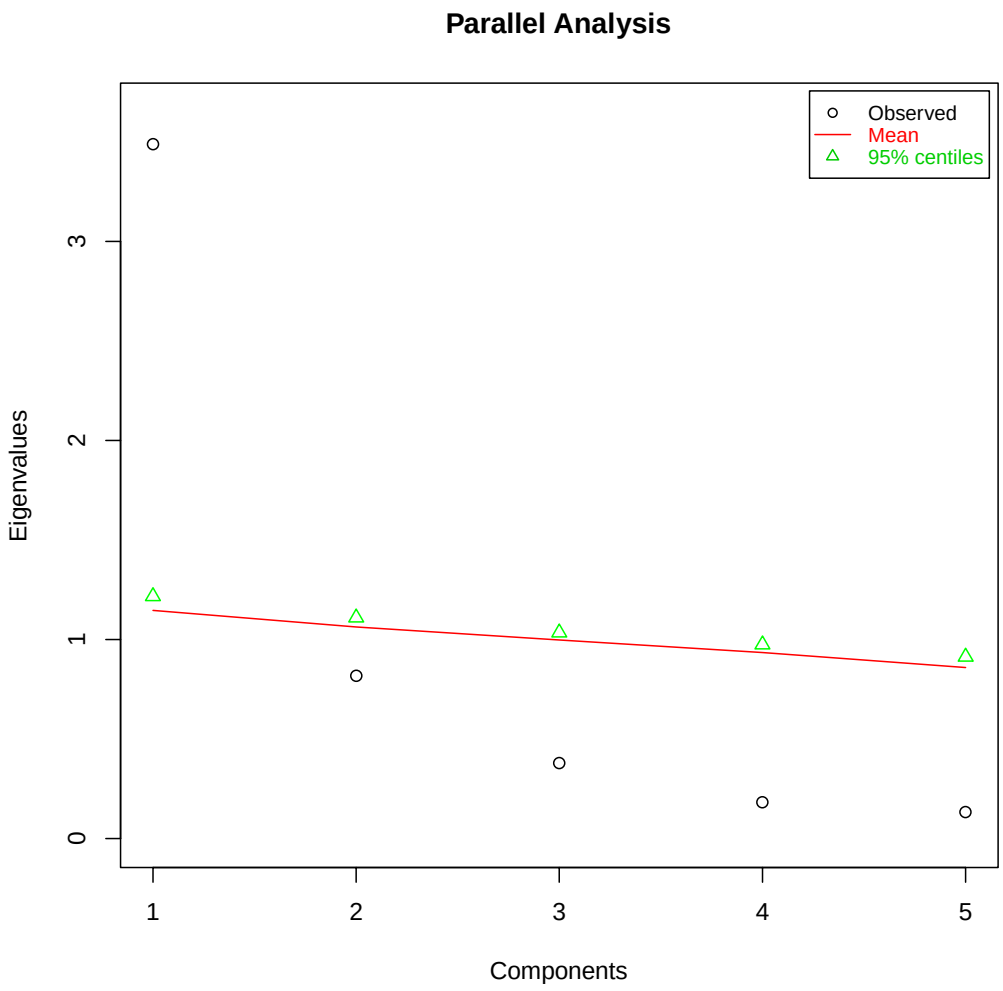



*Figure 10 - Parallel analysis for final PCA, showing that only one factor should be retained.*

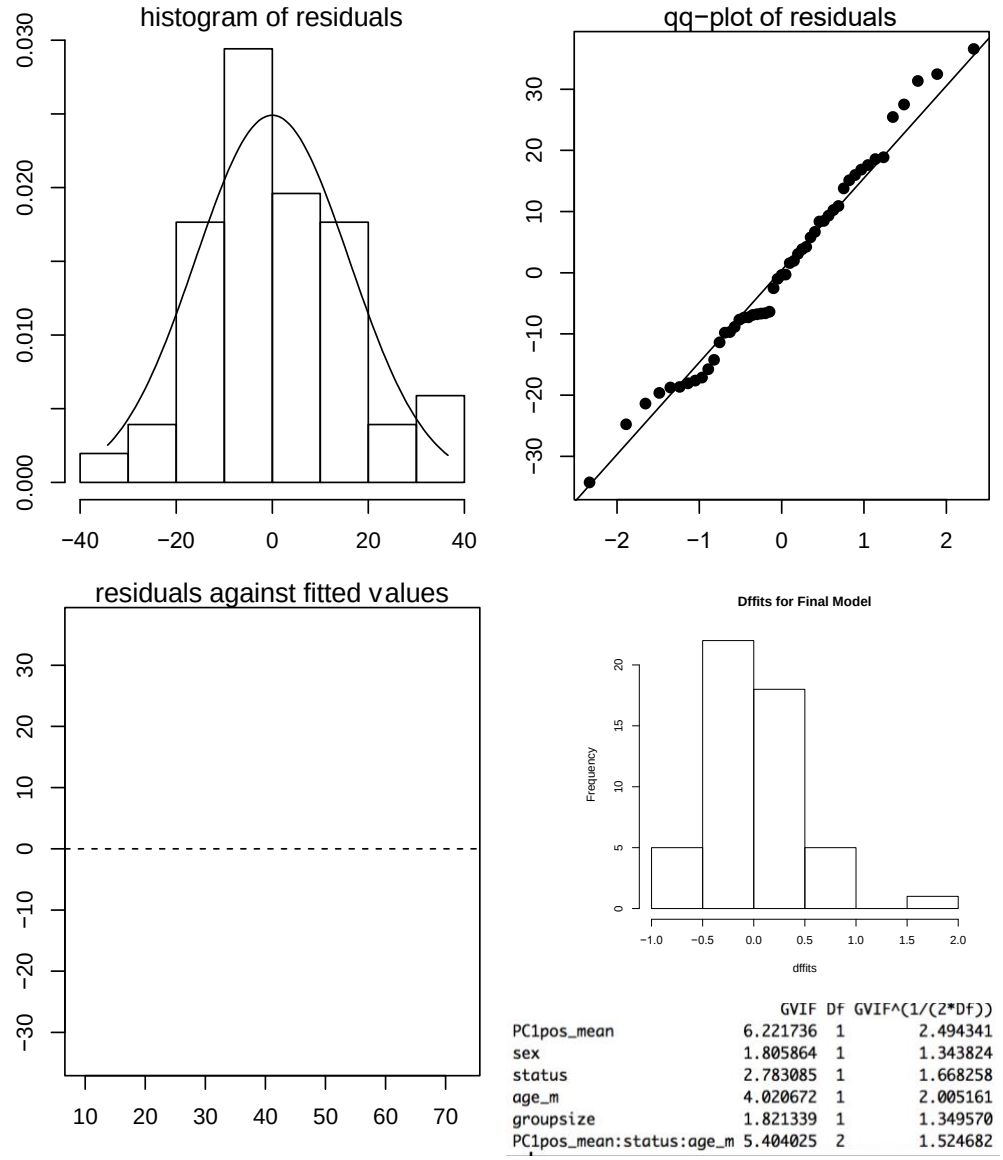
# APPENDIX D – Hand-bias chi-squares

*Table 8 - χ2 results showing individuals with significant hand bias and corresponding values.*

| Name | χ2 | Significant? |
|---|---|---|
| James | 0.000 | No |
| Manuka | 0.104 | No |
| Nautilus | 5.833 | Yes |
| Nebula | 15.360 | Yes |
| Lily | 0.101 | No |
| Nando | 0.133 | No |
| Vesta | 0.000 | No |
| Vito | 0.000 | No |
| Jaja | 0.196 | No |
| Jandira | 0.938 | No |
| Jelly | 1.765 | No |
| Membo | 0.000 | No |
| Wasabi | 0.104 | No |
| Washington | 17.071 | Yes |
| Werewolf | 0.938 | No |
| Wolverine | 1.637 | No |
| Lancia | 13.297 | Yes |
| Lexus | 2.771 | No |
| Lola | 1.823 | No |
| Lotus | 1.200 | No |
| Conan | 8.181 | Yes |
| Madame | 0.573 | No |
| Madita | 1.707 | No |
| Mulan | 0.104 | No |
| Lex | 0.000 | No |
| Nougat | 19.649 | Yes |
| Nox | 0.409 | No |
| Nux | 0.104 | No |
| Garetta | 0.693 | No |
| Nuno | 0.502 | No |
| Tabor | 0.502 | No |
| Wisconsin | 10.025 | Yes |
| Wombat | 0.501 | No |
| Jamaica | 0.101 | No |
| Jambi | 8.025 | Yes |

| | | |
|---|---|---|
| Jupie | 1.200 | No |
| Marvin | 0.196 | No |
| John | 2.747 | No |
| Merkur | 0.119 | No |
| Mina | 0.914 | No |
| Mojita | 5.161 | Yes |
| Narnia | 0.119 | No |
| Nirvana | 0.427 | No |
| Tamino | 0.000 | No |
| Lea | 0.104 | No |
| Lima | 1.706 | No |
| Lynx | 0.000 | No |
| Craken | 0.000 | No |
| Ginger | 0.104 | No |
| Grappa | 3.333 | No |
| Guapa | 0.501 | No |

# APPENDIX E – Model diagnostics




| | GVIF | Df | GVIF^(1/(2*Df)) |
|---|---|---|---|
| PC1pos_mean | 6.221736 | 1 | 2.494341 |
| sex | 1.805864 | 1 | 1.343824 |
| status | 2.783085 | 1 | 1.668258 |
| age_m | 4.020672 | 1 | 2.005161 |
| groupsize | 1.821339 | 1 | 1.349570 |
| PC1pos_mean:status:age_m | 5.404025 | 2 | 1.524682 |

*Figure 11 - Model diagnostics*

# References


Abreu, F., De la Fuente, M. F. C., Schiel, N., & Souto, A. (2016). Feeding ecology and behavioral adjustments: flexibility of a small neotropical primate (Callithrix jacchus) to survive in a semiarid environment. *Mammal Research*, *61*(3), 221–229. https://doi.org/10.1007/s13364-016-0262-4

Addessi, E., Chiarotti, F., & Visalberghi, E. (2007). Response to novel food and the role of social influences in Common Marmosets (*Callithrix jacchus*) and Goeldi's Monkeys (*Callimico goeldii*). *American Journal of Primatology*, *1222*(11), 1210–1222. https://doi.org/10.1002/ajp

Addessi, E., Mancini, A., Crescimbene, L., & Visalberghi, E. (2011). How social context, token value, and time course affect token exchange in capuchin monkeys (Cebus apella). *International Journal of Primatology*, *32*(1), 83–98. https://doi.org/10.1007/s10764-010-9440-4

Akinshina, N. G., Azizov, A. A., Shtonda, N. I., Khalmurzayeva, A. I., & Rakhmatullina, N. S. (2018). Ecological plasticity of the photosynthetic apparatus of hibiscus syriacus L. under Pressure of high temperature, insolation, and air pollution. *Moscow University Biological Sciences Bulletin*, *73*(3), 162–171. https://doi.org/10.3103/S0096392518030021

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, *18*(18), 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Amici, F., Call, J., Watzek, J., Brosnan, S., & Aureli, F. (2018). Social inhibition and behavioural flexibility when the context changes: A comparison across six primate species. *Scientific Reports*, *8*(1), 1–9. https://doi.org/10.1038/s41598-018-21496-6

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Counting conformity: Evaluating the units of information in frequency-dependent social learning. *Animal Behaviour*, *110*, e5–e8. https://doi.org/10.1016/j.anbehav.2015.09.015

Aplin, L. M., Sheldon, B. C., & McElreath, R. (2017). Conformity does not perpetuate suboptimal

traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(30), 7830–7837. https://doi.org/10.1073/pnas.1621067114

Arvidsson, L. K., & Matthysen, E. (2016). Individual differences in foraging decisions: Information-gathering strategies or flexibility? *Behavioral Ecology*, *27*(5), 1353–1361. https://doi.org/10.1093/beheco/arw054

Audet, J.-N., & Lefebvre, L. (2017). What's flexible in behavioral flexibility? *Behavioral Ecology*, *28*(4), 943–947. https://doi.org/10.1093/beheco/arx007

Auersperg, A. M. I., Szabo, B., Von Bayern, A. M. P., & Kacelnik, A. (2012). Spontaneous innovation in tool manufacture and use in a Goffin's cockatoo. *Current Biology*, *22*(21). https://doi.org/10.1016/j.cub.2012.09.002

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., … Van Schaik, C. P. (2008). Fission-fusion dynamics new research frameworks. *Current Anthropology*, *49*(4), 627–654. https://doi.org/10.1086/586708

Ayala, D., Acevedo, P., Pombi, M., Dia, I., Boccolini, D., Costantini, C., … Fontenille, D. (2017). Chromosome inversions and ecological plasticity in the main African malaria mosquitoes. *Evolution*, *71*(3), 686–701. https://doi.org/10.1111/evo.13176

Badihi, I. (2006). *The effects of complexity, choice and control on the behaviour and the welfare of captive common marmosets (Callithrix jacchus)*. University of Stirling. https://doi.org/10.1258/002367796780739853

Baker, P. M., Raynor, S. A., Francis, N. T., & Mizumori, S. J. Y. (2017). Lateral habenula integration of proactive and retroactive information mediates behavioral flexibility. *Neuroscience*, *345*, 89–98. https://doi.org/10.1016/j.neuroscience.2016.02.010

Banta, T. J. (1970). Tests for the evaluation of early child-hood education: the Cincinnati Autonomy Test Battery. In J. Hellmuth (Ed.), *Cognitive Studies* (1st ed.).

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(25), 6506–6511. https://doi.org/10.1073/pnas.1711842115

Barbaresi, S., Santini, G., Tricarico, E., & Gherardi, F. (2004). Ranging behaviour of the invasive

crayfish, Procambarus clarkii (Girard). *Journal of Natural History*, *38*(22), 2821–2832. https://doi.org/10.1080/00222930410001663308

Barbosa, M. N., & da Silva Mota, M. T. (2013). Alloparental responsiveness to newborns by nonreproductive, adult male, common marmosets (Callithrix jacchus). *American Journal of Primatology*, *75*(2), 145–152. https://doi.org/10.1002/ajp.22092

Bardier, G., Aisenberg, A., Toscano-Gadea, C. A., & Costa, F. G. (2015). Wooing during day or night is not the same: An experimental study in the wolf spider Schizocosa malitiosa. *Ethology*, *121*(10), 958–965. https://doi.org/10.1111/eth.12408

Beck, B. B., Kleiman, D. G., Dietz, J. M., Castro, I., Carvalho, C., Martins, A., & Rettberg-Beck, B. (1991). Losses and reproduction in reintroduced golden lion tamarins, Leontopithecus rosalia. *Dodo*, (27), 50–61.

Beesley, T., Nguyen, K. P., Pearson, D., & Le Pelley, M. E. (2015). Uncertainty and predictiveness determine attention to cues during human associative learning. *Quarterly Journal of Experimental Psychology*, *68*(11), 2175–2199. https://doi.org/10.1080/17470218.2015.1009919

Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087–4095. https://doi.org/10.1098/rspb.2012.1450

Benson-Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, Crocuta crocuta. *Animal Behaviour*, *85*(2), 349–356. https://doi.org/10.1016/j.anbehav.2012.11.003

Beran, M. J., & Evans, T. A. (2012). Language-trained chimpanzees (Pan troglodytes) delay gratification by choosing token exchange over immediate reward consumption. *American Journal of Primatology*, *74*(9), 864–870. https://doi.org/10.1002/ajp.22042

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (Papio ursinus) and geladas (Theropithecus gelada). *Animal Cognition*, *12*(1), 63–73. https://doi.org/10.1007/s10071-008-0171-2

Bering, J. M. (2004). A critical review of the “enculturation hypothesis”: The effects of human rearing on great ape social cognition. *Animal Cognition*, *7*(4), 201–212.

https://doi.org/10.1007/s10071-004-0210-6

Berlyne, D. E. (1950). Novelty and curiosity as determinants of exploratory behaviour. *British Journal of Psychology. General Section*, *41*(1–2), 68–80. https://doi.org/10.1111/j.2044-8295.1950.tb00262.x

Berlyne, D. E. (1955). The arousal and satiation of perceptual curiosity in the rat. *Journal of Comparative and Physiological Psychology*, *48*(4), 238–246. https://doi.org/10.1037/h0042968

Bevacqua, S., Cerasti, E., Falcone, R., Cervelloni, M., Brunamonti, E., Ferraina, S., & Genovesio, A. (2013). Macaque monkeys can learn token values from human models through vicarious reward. *PLoS ONE*, *8*(3), e59961. https://doi.org/10.1371/journal.pone.0059961

Bezerra, B. M., & Souto, A. (2008). Structure and usage of the vocal repertoire of Callithrix jacchus. *International Journal of Primatology*, *29*(3), 671–701. https://doi.org/10.1007/s10764-008-9250-0

Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (Milvago chimango). *Animal Cognition*, *13*(5), 701–710. https://doi.org/10.1007/s10071-010-0319-8

Biondi, L. M., Guido, J. M., Bó, M. S., Muzio, R. N., & Vassallo, A. I. (2015). The role of stimulus complexity, age and experience in the expression of exploratory behaviour in the Chimango Caracara, Milvago chimango. *Animal Cognition*, *18*(1), 139–150. https://doi.org/10.1007/s10071-014-0785-5

Bird, C. D., & Emery, N. J. (2009). Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(25), 10370–10375. https://doi.org/10.1073/pnas.0901008106

Biro, D., Carvalho, S., & Matsuzawa, T. (2010). Tools, traditions, and technologies: interdisciplinary approaches to chimpanzee nut cracking. In E. V. Lonsdorf, S. R. Ross, & T. Matsuzawa (Eds.), *The Mind of the Chimpanzee: Ecological and Experimental Perspectives* (pp. 141–155). University of Chicago Press.

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate

promote consistent individual differences in behavior? *Trends in Ecology and Evolution*, *25*(11), 653–659. https://doi.org/10.1016/j.tree.2010.08.003

Bitterman, M. E., Sutherland, N. S., & Mackintosh, N. J. (1972). Mechanisms of animal discrimination learning. *The American Journal of Psychology*, *85*(2), 301. https://doi.org/10.2307/1420674

Bjorklund, D., & Kipp, K. (2002). *Social cognition, inhibition, and theory of mind: The evolution of human intelligence*. Mahwah, NJ: Lawrence Erlbaum Associate Publishers.

Blumroeder, J., Eccard, J. A., & Blaum, N. (2012). Behavioural flexibility in foraging mode of the spotted sand lizard (Pedioplanis l. lineoocellata) seems to buffer negative impacts of savanna degradation. *Journal of Arid Environments*, *77*(1), 149–152. https://doi.org/10.1016/j.jaridenv.2011.10.005

Bodensteiner, K. J., Cain, P., Ray, A. S., & Hamula, L. A. (2006). Effects of pregnancy on spatial cognition in female Hooded Long-Evans rats. *Hormones and Behavior*, *49*(3), 303–314. https://doi.org/10.1016/j.yhbeh.2005.08.002

Boesch, C., Hohmann, G., & Marchant, L. F. (Eds.). (2002). *Behavioural diversity in chimpanzees and bonobos*. Cambridge: Cambridge University Press.

Bolhuis, J. E., Schouten, W. G. P., Leeuw, J. A. De, Schrama, J. W., & Wiegant, V. M. (2004). Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behavioural Brain Research*, *152*(2), 351–360. https://doi.org/10.1016/j.bbr.2003.10.024

Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica). *Journal of Comparative Psychology*, *121*(4), 372–379. https://doi.org/10.1037/0735-7036.121.4.372

Bonnie, K. E., Milstein, M. S., Calcutt, S. E., Ross, S. R., Wagner, K. E., & Lonsdorf, E. V. (2012). Flexibility and persistence of chimpanzee (Pan troglodytes) foraging behavior in a captive environment. *American Journal of Primatology*, *74*(7), 661–668. https://doi.org/10.1002/ajp.22020

Boogert, Neeltje J., Reader, S. M., Hoppitt, W., & Laland, K. N. (2008). The origin and spread of innovations in starlings. *Animal Behaviour*, *75*(4), 1509–1518.

https://doi.org/10.1016/j.anbehav.2007.09.033

Boogert, Neeltje J., Reader, S. M., & Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, *72*(6), 1229–1239. https://doi.org/10.1016/j.anbehav.2006.02.021

Boogert, Neeltje Janna, Monceau, K., & Lefebvre, L. (2010). A field test of behavioural flexibility in Zenaida doves (Zenaida aurita). *Behavioural Processes*, *85*(2), 135–141. https://doi.org/10.1016/j.beproc.2010.06.020

Borrego, N., & Gaines, M. (2016). Social carnivores outperform asocial carnivores on an innovative problem. *Animal Behaviour*, *114*, 21–26. https://doi.org/10.1016/j.anbehav.2016.01.013

Bourjade, M., Call, J., Pelé, M., Maumy, M., & Dufour, V. (2014). Bonobos and orangutans, but not chimpanzees, flexibly plan for the future in a token-exchange task. *Animal Cognition*, *17*(6), 1329–1340. https://doi.org/10.1007/s10071-014-0768-6

Boysen, S. T., Kuhlmeier, V. A., Halliday, P., & Halliday, Y. M. (2009). Tool use in captive gorillas. In S. T. Parker (Ed.), *The Mentalities of Gorillas and Orangutans* (pp. 179–187). Cambridge Core. https://doi.org/10.1017/cbo9780511542305.009

Brooks, K. C., Maia, R., Duffy, J. E., Hultgren, K. M., & Rubenstein, D. R. (2017). Ecological generalism facilitates the evolution of sociality in snapping shrimps. *Ecology Letters*, *20*(12), 1516–1525. https://doi.org/10.1111/ele.12857

Brosnan, S. F., & DeWaal, F. B. M. (2001). Regulation of vocal output by chimpanzees finding food in the presence or absence of an audience. *Evolution of CommunicationEvolution of Communication An International Multidisciplinary Journal*, *4*(2), 211–224. https://doi.org/10.1075/eoc.4.2.05bro

Brosnan, S. F., & Hopper, L. M. (2014). Psychological limits on animal innovation. *Animal Behaviour*, *92*, 325–332. https://doi.org/10.1016/j.anbehav.2014.02.026

Brown, G. R., Almond, R. E. A., & Bergen, Y. van. (2004). Begging, stealing, and offering: Food transfer in nonhuman primates. *Advances in the Study of Behavior*, *34*, 265–295. https://doi.org/10.1016/S0065-3454(04)34007-6

Brucks, D., Marshall-Pescini, S., Wallis, L. J., Huber, L., & Range, F. (2017). Measures of dogs'

inhibitory control abilities do not correlate across tasks. *Frontiers in Psychology*, *8*(MAY), 1–17. https://doi.org/10.3389/fpsyg.2017.00849

Brügger, R. K., Kappeler-Schmalzriedt, T., & Burkart, J. M. (2018). Reverse audience effects on helping in cooperatively breeding marmoset monkeys. *Biology Letters*, *14*(3). https://doi.org/10.1098/rsbl.2018.0030

Brust, V., Wuerz, Y., & Krüger, O. (2013). Behavioural flexibility and personality in zebra finches. *Ethology*, *119*(7), 559–569. https://doi.org/10.1111/eth.12095

Bublitz, A., Weinhold, S. R., Strobel, S., Dehnhardt, G., & Hanke, F. D. (2017). Reconsideration of serial visual reversal learning in octopus (Octopus Vulgaris) from a methodological perspective. *Frontiers in Physiology*, *8*(FEB). https://doi.org/10.3389/fphys.2017.00054

Buckner, J. C., Lynch Alfaro, J. W., Rylands, A. B., & Alfaro, M. E. (2015). Biogeography of the marmosets and tamarins (Callitrichidae). *Molecular Phylogenetics and Evolution*, *82*(PB), 413–425. https://doi.org/10.1016/j.ympev.2014.04.031

Bugnyar, T., & Heinrich, B. (2006). Pilfering ravens, Corvus corax, adjust their behaviour to social context and identity of competitors. *Animal Cognition*, *9*(4), 369–376. https://doi.org/10.1007/s10071-006-0035-6

Bugnyar, T., & Huber, L. (1997). Push or pull: An experimental study on imitation in marmosets. *Animal Behaviour*, *54*(4), 817–831. https://doi.org/10.1006/anbe.1996.0497

Bugnyar, T., & Kotrschal, K. (2004). Leading a conspecffic away from food in ravens (Corvus corax)? *Animal Cognition*, *7*(2), 69–76. https://doi.org/10.1007/s10071-003-0189-4

Bunnell, B. N., Gore, W. T., & Perkins, M. N. (1980). Performance correlates of social behavior and organization: Social rank and reversal learning in crab-eating macaques (M. fascicularis). *Primates*, *21*(3), 376–388. https://doi.org/10.1007/BF02390467

Burkart, J. M. (2009). Socio-cognitive abilities and cooperative breeding. In L. S. Röska-Hardy & E. M. Neumann-Held (Eds.), *Learning from Animals?: Examining the Nature of Human Uniqueness* (pp. 123–141). New York: Psychology Press. https://doi.org/10.4324/9780203889909

Burkart, J. M. (2015). Opposite effects of male and female helpers on social tolerance and proactive prosociality in callitrichid family groups. *Scientific Reports*, *5*, 1–9.

https://doi.org/10.1038/srep09622

Burkart, J. M., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*, *104*(50), 19762–19766. https://doi.org/10.1073/pnas.0710310104

Burkart, J. M., & Heschl, A. (2006). Geometrical gaze following in common marmosets (Callithrix jacchus). *Journal of Comparative Psychology*, *120*(2), 120–130. https://doi.org/10.1037/0735-7036.120.2.120

Burkart, J. M., & Heschl, A. (2007). Understanding visual access in common marmosets, Callithrix jacchus: perspective taking or behaviour reading? *Animal Behaviour*, *73*(3), 457–469. https://doi.org/10.1016/j.anbehav.2006.05.019

Burkart, J. M., Hrdy, S. B., & van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, *18*(5), 175–186. https://doi.org/10.1002/evan.20222

Burkart, J. M., Kupferberg, A., Glasauer, S., & van Schaik, C. P. (2012). Even simple forms of social learning rely on intention attribution in marmoset monkeys (Callithrix jacchus). *Journal of Comparative Psychology*, *126*(2), 129–138. https://doi.org/10.1037/a0026025

Burkart, J. M., Strasser, A., & Foglia, M. (2009). Trade-offs between social learning and individual innovativeness in common marmosets, Callithrix jacchus. *Animal Behaviour*, *77*(5), 1291–1301. https://doi.org/10.1016/j.anbehav.2009.02.006

Burkart, J. M., & van Schaik, C. P. (2010). Cognitive consequences of cooperative breeding in primates? *Animal Cognition*, *13*(1), 1–19. https://doi.org/10.1007/s10071-009-0263-7

Burkart, J. M., & van Schaik, C. P. (2016). Revisiting the consequences of cooperative breeding. *Journal of Zoology*, *299*(2), 77–83. https://doi.org/10.1111/jzo.12322

Byrne, R. W. (2013). Animal curiosity. *Current Biology*, *23*(11). https://doi.org/10.1016/j.cub.2013.02.058

Cacchione, T., & Burkart, J. M. (2012). Dissociation between seeing and acting: Insights from common marmosets (Callithrix jacchus). *Behavioural Processes*, *89*(1), 52–60. https://doi.org/10.1016/j.beproc.2011.10.010

Caldwell, C. A., & Whiten, A. (2003). Scrounging facilitates social learning in common marmosets, Callithrix jacchus. *Animal Behaviour*, *65*(6), 1–8. https://doi.org/10.1006/anbe.2003.2145

Caldwell, C. A., & Whiten, A. (2004). Testing for social learning and imitation in common marmosets, Callithrix jacchus, using an artificial fruit. *Animal Cognition*, *7*(2), 77–85. https://doi.org/10.1007/s10071-003-0192-9

Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (Callithrix jacchus): Problem solving and responses in a novel setting. *Journal of Comparative Psychology*, *113*(2), 149–157. https://doi.org/10.1037/0735-7036.113.2.149

Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, *117*(5), 641–653. https://doi.org/10.1111/j.0030-1299.2008.16513.x

Careau, V., Thomas, D., Pelletier, F., Turki, L., Landry, F., Garant, D., & Réale, D. (2011). Genetic correlation between resting metabolic rate and exploratory behaviour in deer mice (Peromyscus maniculatus). *Journal of Evolutionary Biology*, *24*(10), 2153–2163. https://doi.org/10.1111/j.1420-9101.2011.02344.x

Carere, C., & Locurto, C. (2011). Interaction between animal personality and animal cognition. *Current Zoology*, *57*(4), 491–498. https://doi.org/10.1093/czoolo/57.4.491

Carere, C., & Maestripieri, D. (2013). Animal personalities. In *Animal Personalities* (pp. 1–9). https://doi.org/10.7208/chicago/9780226922065.003.0001

Čarni, A., Matevski, V., & Šilc, U. (2010). Morphological, chorological and ecological plasticity of Cistus incanus in the southern balkans. *Plant Biosystems*, *144*(3), 602–617. https://doi.org/10.1080/11263504.2010.489328

Carr, K., Kendal, R. L., & Flynn, E. G. (2015). Imitate or innovate? Children's innovation is influenced by the efficacy of observed behaviour. *Cognition*, *142*, 322–332. https://doi.org/10.1016/j.cognition.2015.05.005

Carr, K., Kendal, R. L., & Flynn, E. G. (2016). Eureka!: What is innovation, how does it develop, and who does it? *Child Development*, *87*(5), 1505–1519. https://doi.org/10.1111/cdev.12549

Castro, C. S. S. De, & Araújo, A. (2006). Diet and feeding behaviour of marmoset, Callithrix

jacchus. *Revista Brasileira de Ecologia, 7*, 14-19.

Chan, A. D. F., Nippak, P. M. D., Murphey, H., Ikeda-Douglas, C. J., Muggenburg, B., Head, E., … Milgram, N. W. (2002). Visuospatial impairments in aged canines (Canis familiaris): The role of cognitive-behavioral flexibility. *Behavioral Neuroscience*, *116*(3), 443–454. https://doi.org/10.1037/0735-7044.116.3.443

Chao, L. L., & Knight, R. T. (1997). Prefrontal deficits in attention and inhibitory control with aging. *Cerebral Cortex*, *7*(1), 63–69. https://doi.org/10.1093/cercor/7.1.63

Chevalier-Skolnikoff, S., & Liska, J. (1993). Tool use by wild and captive elephants. *Animal Behaviour*, *46*(2), 209–219. https://doi.org/10.1006/anbe.1993.1183

Chittka, L., & Niven, J. (2009). Are bigger brains better? *Current Biology*. https://doi.org/10.1016/j.cub.2009.08.023

Chow, P. K. Y., Leaver, L. A., Wang, M., & Lea, S. E. G. (2017). Touch screen assays of behavioural flexibility and error characteristics in Eastern grey squirrels (Sciurus carolinensis). *Animal Cognition*, *20*(3), 459–471. https://doi.org/10.1007/s10071-017-1072-z

Chun, M. M., & Turk-Browne, N. B. (2007). Interactions between attention and memory. *Current Opinion in Neurobiology*, *17*(2), 177–184. https://doi.org/10.1016/j.conb.2007.03.005

Colgan, P. (1989). *Animal motivation*. *Animal Behaviour Series*. New York and London: Chapman and Hall. https://doi.org/10.1007/978-94-009-0831-4

Collins, P., Wilkinson, L. S., Everitt, B. J., Robbins, T. W., & Roberts, A. C. (2000). The effect of dopamine depletion from the caudate nucleus of the common marmoset (Callithrix jacchus) on tests of prefrontal cognitive function. *Behavioral Neuroscience*, *114*(1), 3–17. https://doi.org/10.1037/0735-7044.114.1.3

Coppens, C. M., De Boer, S. F., & Koolhaas, J. M. (2010). Coping styles and behavioural flexibility: Towards underlying mechanisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rstb.2010.0217

Couchoux, C., & Cresswell, W. (2012). Personality constraints versus flexible antipredation behaviors: How important is boldness in risk management of redshanks (Tringa totanus)

foraging in a natural system? *Behavioral Ecology*, *23*(2), 290–301. https://doi.org/10.1093/beheco/arr185

Cronin, K. A., Kurian, A. V., & Snowdon, C. T. (2005). Cooperative problem solving in a cooperatively breeding primate (Saguinus oedipus). *Animal Behaviour*, *69*(1), 133–142. https://doi.org/10.1016/j.anbehav.2004.02.024

Cronin, K. A., Pieper, B. A., Van Leeuwen, E. J. C., Mundry, R., & Haun, D. B. M. (2014). Problem solving in the presence of others: How rank and relationship quality impact resource acquisition in chimpanzees (Pan troglodytes). *PLoS ONE*, *9*(4). https://doi.org/10.1371/journal.pone.0093204

Croston, R., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., Parchman, T. L., & Pravosudov, V. V. (2017). Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. *Animal Behaviour*, *123*, 139–149. https://doi.org/10.1016/j.anbehav.2016.10.004

da Silva Mota, M. T., Franci, C. R., & De Sousa, M. B. C. (2006). Hormonal changes related to paternal and alloparental care in common marmosets (Callithrix jacchus). *Hormones and Behavior*, *49*(3), 293–302. https://doi.org/10.1016/j.yhbeh.2005.07.012

Dall, S. R. X. (2004). Behavioural biology: Fortune favours bold and shy personalities. *Current Biology*. https://doi.org/10.1016/j.cub.2004.06.011

Damerius, L. A., Forss, S. I. F., Kosonen, Z. K., Willems, E. P., Burkart, J. M., Call, J., … Van Schaik, C. P. (2017). Orientation toward humans predicts cognitive performance in orang-utans. *Scientific Reports*, *7*. https://doi.org/10.1038/srep40052

Damerius, L. A., Graber, S. M., Willems, E. P., & van Schaik, C. P. (2017). Curiosity boosts orang-utan problem-solving ability. *Animal Behaviour*, *134*, 57–70. https://doi.org/10.1016/j.anbehav.2017.10.005

Day, R. L., Coe, R. L., Kendal, J. R., & Laland, K. N. (2003). Neophilia, innovation and social learning: A study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, *65*(3), 559–571. https://doi.org/10.1006/anbe.2003.2074

de Waal, F. B. M., & Tyack, P. L. (Eds.). (2003). *Animal social complexity: Intelligence, culture, and individualized societies*. London: Harvard University Press.

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science*, *335*(6072), 1114–1118. https://doi.org/10.1126/science.1213969

Deaner, R. O., Isler, K., Burkart, J. M., & Van Schaik, C. P. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior and Evolution*, *70*(2), 115–124. https://doi.org/10.1159/000102973

Deaner, R. O., Schaik, C. P. Van, & Johnson, V. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology*, *4*, 149–196. https://doi.org/10.1556/JEP.2007.1013

Dettling, A. C., Feldon, J., & Pryce, C. R. (2002). Early deprivation and behavioral and physiological responses to social separation/novelty in the marmoset. *Pharmacology Biochemistry and Behavior*, *73*(1), 259–269. https://doi.org/10.1016/S0091-3057(02)00785-2

Díaz, M. (1994). Variability in seed size selection by granivorous passerines: effects of bird size, bird size variability, and ecological plasticity. *Oecologia*, *99*(1–2), 1–6. https://doi.org/10.1007/BF00317076

Dillis, C., Humle, T., & Snowdon, C. T. (2010). Socially biased learning among adult cottontop tamarins (Saguinus oedipus). *American Journal of Primatology*, *72*(4), 287–295. https://doi.org/10.1002/ajp.20778

Dindo, M., Whiten, A., & De Waal, F. (2009). Social facilitation of exploratory foraging behavior in capuchin monkeys (Cebus apella). *American Journal of Primatology*, *71*(5), 419–426. https://doi.org/10.1002/ajp.20669

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution*, *25*(2), 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: Causes and consequences. *Animal Behaviour*, *85*(5), 1031–1039. https://doi.org/10.1016/j.anbehav.2012.12.032

Diquelou, M. C., Griffin, A. S., & Sol, D. (2016). The role of motor diversity in foraging

innovations: A cross-species comparison in urban birds. *Behavioral Ecology*, *27*(2), 584–591. https://doi.org/10.1093/beheco/arv190

Drea, C. M. (1998). Status, age, and sex effects on performance of discrimination tasks in group-tested rhesus monkeys (Macaca mulatta). *Journal of Comparative Psychology*, *112*(2), 170–182. https://doi.org/10.1037/0735-7036.112.2.170

Duckworth, R. A. (2010). Evolution of personality: Developmental constraints on behavioral flexibility. *The Auk*, *127*(4), 752–758. https://doi.org/10.1525/auk.2010.127.4.752

Dugatkin, L. A., & Alfieri, M. S. (2003). Boldness, behavioral inhibition and learning. *Ethology Ecology and Evolution*, *15*(1), 43–49. https://doi.org/10.1080/08927014.2003.9522689

Dukas, R. (2013). Effects of learning on evolution: Robustness, innovation and speciation. *Animal Behaviour*, *85*(5), 1023–1030. https://doi.org/10.1016/j.anbehav.2012.12.030

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, *22*(6), 469–493. https://doi.org/10.1016/0047-2484(92)90081-J

Dunbar, R. I. M., & Bever, J. (2010). Neocortex size predicts group size in carnivores and some insectivores. *Ethology*, *104*(8), 695–708. https://doi.org/10.1111/j.1439-0310.1998.tb00103.x

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*(5843), 1344–1347. https://doi.org/10.1126/science.1145463

Easdale, L. C., Le Pelley, M. E., & Beesley, T. (2019). The onset of uncertainty facilitates the learning of new associations by increasing attention to cues. *Quarterly Journal of Experimental Psychology (2006)*, *72*(2), 193–208. https://doi.org/10.1080/17470218.2017.1363257

Ebel, S. J., & Call, J. (2018). The interplay of prior experience and motivation in great ape problem-solving (Gorilla gorilla, Pan paniscus, Pan troglodytes, and Pongo abelii). *Journal of Comparative Psychology*, *132*(3), 294–305. https://doi.org/10.1037/com0000117

Edgell, T. C., Lynch, B. R., Trussell, G. C., & Palmer, A. R. (2009). Experimental evidence for the rapid evolution of behavioral canalization in natural populations. *The American Naturalist*, *174*(3), 434–440. https://doi.org/10.1086/603639

Eggert, A.-K. (2017). Cooperative breeding in insects and vertebrates. In *Evolutionary Biology*.

Oxford University Press. https://doi.org/10.1093/OBO/9780199941728-0024

Epple, G. (1970). Maintenance, breeding, and development of marmoset monkeys (Callithricidae) in captivity. *Folia Primatologica*, *12*(1), 56–76. https://doi.org/10.1159/000155281

Evans, T. A., Perdue, B. M., Parrish, A. E., Menzel, E. C., Brosnan, S. F., & Beran, M. J. (2012). How is chimpanzee self-control influenced by social setting? *Scientifica*, *2012*, 1–9. https://doi.org/10.6064/2012/654094

Fagen, R. (1982). Evolutionary issues in development of behavioral flexibility. In P. Bateson & K. P. H. (Eds.), *Perspectives in Ethology: Ontogeny* (pp. 365–383). Springer.

Fagnani, J., Barrera, G., Carballo, F., & Bentosela, M. (2016). Is previous experience important for inhibitory control? A comparison between shelter and pet dogs in A-not-B and cylinder tasks. *Animal Cognition*, *19*(6), 1165–1172. https://doi.org/10.1007/s10071-016-1024-z

Faustino, A. I., Oliveira, G. A., & Oliveira, R. F. (2015). Linking appraisal to behavioral flexibility in animals: Implications for stress research. *Frontiers in Behavioral Neuroscience*, *9*(104), 1–7. https://doi.org/10.3389/fnbeh.2015.00104

Finkenwirth, C., Martins, E., Deschner, T., & Burkart, J. M. (2016). Oxytocin is associated with infant-care behavior and motivation in cooperatively breeding marmoset monkeys. *Hormones and Behavior*, *80*, 10–18. https://doi.org/10.1016/j.yhbeh.2016.01.008

Finkler, H., Gunther, I., & Terkel, J. (2011). Behavioral differences between urban feeding groups of neutered and sexually intact free-roaming cats following a trap-neuter-return procedure. *Journal of the American Veterinary Medical Association*, *238*(9), 1141–1149. https://doi.org/10.2460/javma.238.9.1141

Floresco, S. B., Zhang, Y., & Enomoto, T. (2009). Neural circuits subserving behavioral flexibility and their relevance to schizophrenia. *Behavioural Brain Research*, *204*(2), 396–409. https://doi.org/10.1016/j.bbr.2008.12.001

Ford, S. M., Porter, L. M., Davis, L. C., & Tuttle, R. H. (2009). *The smallest anthropoids*. (S. M. Ford, L. M. Porter, & L. C. Davis, Eds.), *The Smallest Anthropoids*. Boston, MA: Springer US. https://doi.org/10.1007/978-1-4419-0293-1

Forss, S. I. F., Willems, E., Call, J., & Van Schaik, C. P. (2016). Cognitive differences between

orang-utan species: A test of the cultural intelligence hypothesis. *Scientific Reports*, *6*(April), 1–12. https://doi.org/10.1038/srep30516

Foster, S. A., & Sih, A. (2013). Behavioural plasticity and evolution. *Animal Behaviour*, *85*(5), 1003. https://doi.org/10.1016/j.anbehav.2013.04.006

Fragaszy, D. M., Visalberghi, E., & Robinson, J. G. (1990). Variability and adaptiability in the genus Cebus. *Folia Primatologica*, *54*, 114–118. https://doi.org/10.1248/cpb.15.1470

Fuentes, A. (2004). It's not all sex and violence: Integrated anthropology and the role of cooperation and social complexity in human evolution. *American Anthropologist*, *106*(4), 710–718. https://doi.org/10.1525/aa.2004.106.4.710

Galef, B. G. (2003). Social learning: Promoter or inhibitor of innovation. In S. M. Reader & K. N. Laland (Eds.), *Animal Innovation* (pp. 137–155). Cambridge University Press.

Gapp, K., Soldado-Magraner, S., Alvarez-Sánchez, M., Bohacek, J., Vernaz, G., Shu, H., … Mansuy, I. M. (2014). Early life stress in fathers improves behavioural flexibility in their offspring. *Nature Communications*, *5*(5466). https://doi.org/10.1038/ncomms6466

Garbino, G. S. T., & Martins-Junior, A. M. G. (2018). Phenotypic evolution in marmoset and tamarin monkeys (Cebidae, Callitrichinae) and a revised genus-level classification. *Molecular Phylogenetics and Evolution*, *118*, 156–171. https://doi.org/10.1016/j.ympev.2017.10.002

Gilhooly, K. J., Fioratou, E., Anthony, S. H., & Wynn, V. (2007). Divergent thinking: Strategies and executive involvement in generating novel uses for familiar objects. *British Journal of Psychology*, *98*, 611–625. https://doi.org/10.1348/096317907X173421

Godfrey-Smith, P. (1996). *Complexity and the function of mind in nature*. Cambridge: Cambridge University Press.

Grabowska, M. J., Steeves, J., Alpay, J., Van De Poll, M., Ertekin, D., & Van Swinderen, B. (2018). Innate visual preferences and behavioral flexibility in Drosophila. *Journal of Experimental Biology*, *221*(23). https://doi.org/10.1242/jeb.185918

Green, J. A., Boyd, I. L., Woakes, A. J., Warren, N. L., & Butler, P. J. (2005). Behavioural flexibility during year-round foraging in macaroni penguins. *Marine Ecology Progress Series*, *296*, 183–196. https://doi.org/10.3354/meps296183

Greenberg, R. (1990). Ecological plasticity, neophobia and resource use in birds. *Studies in Avian Biology*, *13*, 431–437.

Greggor, A. L., Thornton, A., & Clayton, N. S. (2015). Neophobia is not only avoidance: Improving neophobia tests by combining cognition and ecology. *Current Opinion in Behavioral Sciences*, *6*, 82–89. https://doi.org/10.1016/j.cobeha.2015.10.007

Grieco, F., van Noordwijk, A. J., & Visser, M. E. (2002). Evidence for the effect of learning on timing of reproduction in blue tits. *Science*. https://doi.org/10.1126/science.1068287

Griffin, A. S. (2016). Innovativeness as an emergent property: a new alignment of comparative and experimental research on animal innovation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(20150544), 1–9. https://doi.org/http://dx.doi.org/10.1098/rstb.2015.0544

Griffin, A. S., Diquelou, M., & Perea, M. (2014). Innovative problem solving in birds: A key role of motor diversity. *Animal Behaviour*, *92*, 221–227. https://doi.org/10.1016/j.anbehav.2014.04.009

Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes*, *109*(PB), 121–134. https://doi.org/10.1016/j.beproc.2014.08.027

Griffin, A. S., & Guez, D. (2015). Innovative problem solving in nonhuman animals: The effects of group size revisited. *Behavioral Ecology*, *26*(3), 722–734. https://doi.org/10.1093/beheco/aru238

Griffin, A. S., Guez, D., Lermite, F., & Patience, M. (2013). Tracking changing environments: Innovators are fast, but not flexible learners. *PLoS ONE*, *8*(12). https://doi.org/10.1371/journal.pone.0084907

Gruber, T. (2016). Great apes do not learn novel tool use easily: Conservatism, functional fixedness, or cultural influence? *International Journal of Primatology*, *37*(2), 296–316. https://doi.org/10.1007/s10764-016-9902-4

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the Pan lineage. *Animal Behaviour*, *80*(6), 1023–1033. https://doi.org/10.1016/j.anbehav.2010.09.005

Gruber, T., Luncz, L., Mörchen, J., Schuppli, C., Kendal, R. L., & Hockings, K. (2019). Cultural change in animals: a flexible behavioural adaptation to human disturbance. *Palgrave Communications*, *5*(1), 1–9. https://doi.org/10.1057/s41599-019-0271-4

Guerreiro Martins, E. M., Antonio, A. C., Finkenwirth, C., Griesser, M., & Burkart, J. M. (2019). Food sharing patterns in three species of callitrichid monkeys (Callithrix jacchus, Leontopithecus chrysomelas, Saguinus midas): Individual and species differences. *Journal of Comparative Psychology*, *1*(999), 1–14. https://doi.org/10.1037/com0000169

Guido, J. M., Biondi, L. M., Vasallo, A. I., & Muzio, R. N. (2017). Neophobia is negatively related to reversal learning ability in females of a generalist bird of prey, the Chimango Caracara, Milvago chimango. *Animal Cognition*, *20*(4), 591–602. https://doi.org/10.1007/s10071-017-1083-9

Guillette, L. M., Reddon, A. R., Hurd, P. L., & Sturdy, C. B. (2009). Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, Poecile atricapillus. *Behavioural Processes*, *82*(3), 265–270. https://doi.org/10.1016/j.beproc.2009.07.005

Guinote, A. (2007). Power affects basic cognition: Increased attentional inhibition and flexibility. *Journal of Experimental Social Psychology*, *43*(5), 685–697. https://doi.org/10.1016/j.jesp.2006.06.008

Gunhold, T., Massen, J. J. M., Schiel, N., Souto, A., & Bugnyar, T. (2014). Memory, transmission and persistence of alternative foraging techniques in wild common marmosets. *Animal Behaviour*, *91*, 79–91. https://doi.org/10.1016/j.anbehav.2014.02.023

Halsey, L. G., Bezerra, B. M., & Souto, A. S. (2006). Can wild common marmosets (Callithrix jacchus) solve the parallel strings task? *Animal Cognition*, *9*(3), 229–233. https://doi.org/10.1007/s10071-006-0016-9

Hamilton, D. A., & Brigman, J. L. (2015). Behavioral flexibility in rats and mice: Contributions of distinct frontocortical regions. *Genes, Brain and Behavior*. https://doi.org/10.1111/gbb.12191

Hanus, D., Mendes, N., Tennie, C., & Call, J. (2011). Comparing the performances of apes (gorilla gorilla, pan troglodytes, pongo pygmaeus) and human children (homo sapiens) in the

floating peanut task. *PLoS ONE*, *6*(6). https://doi.org/10.1371/journal.pone.0019555

Harding, A. M. A., Piatt, J. F., Schmutz, J. A., Shultz, M. T., Van Pelt, T. I., Kettle, A. B., & Speckman, S. G. (2007). Prey density and the behavioral flexibility of a marine predator: The common murre (Uria aalge). *Ecology*, *88*(8), 2024–2033. https://doi.org/10.1890/06-1695.1

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, *17*(7), 619–623. https://doi.org/10.1016/j.cub.2007.02.040

Harms, M. B., Bowen, K. E. S., Hanson, J. L., & Seth, D. P. (2018). Instrumental learning and cognitive flexibility processes are impaired in children exposed to early life stress. *Developmental Science*, *21*(4).

Harris, T. R., Chapman, C. A., & Monfort, S. L. (2010). Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. *Behavioral Ecology*, *21*(1), 46–56. https://doi.org/10.1093/beheco/arp150

Harrison, R. A., & Whiten, A. (2018). Chimpanzees (Pan troglodytes) display limited behavioural flexibility when faced with a changing foraging task requiring tool use. *PeerJ*, *6*, e4366. https://doi.org/10.7717/peerj.4366

Hauser, M. D., Santos, L. R., Spaepen, G. M., & Pearson, H. E. (2002). Problem solving, inhibition and domain-specific experience: Experiments on cottontop tamarins, Saguinus oedipus. *Animal Behaviour*, *64*(3), 387–396. https://doi.org/10.1006/anbe.2002.3066

Heaton, R. K., Chelune, G. J., Talley, J. L., Kay, G. G., & Curtiss, G. (1993). *Wisconsin card sorting test manual: Revised and expanded*. Odessa, FL: Psychological Assessment Resources Inc. https://doi.org/10.2466/pr0.1995.76.2.623

Hedges, D. W., & Woon, F. L. (2011). Early-life stress and cognitive outcome. *Psychopharmacology*, *214*(1), 121–130. https://doi.org/10.1007/s00213-010-2090-6

Henke-von der Malsburg, J., & Fichtel, C. (2018). Are generalists more innovative than specialists? A comparison of innovative abilities in two wild sympatric mouse lemur species. *Royal Society Open Science*, *5*(8), 180480. https://doi.org/10.1098/rsos.180480

Henshilwood, C. S., D'Errico, F., Yates, R., Jacobs, Z., Tribolo, C., Duller, G. A. T., … Wintle, A. G.

(2002). Emergence of modern human behavior: Middle stone age engravings from South Africa. *Science*, *295*(5558), 1278–1280. https://doi.org/10.1126/science.1067575

Herborn, K. A., Heidinger, B. J., Alexander, L., & Arnold, K. E. (2014). Personality predicts behavioral flexibility in a fluctuating, natural environment. *Behavioral Ecology*, *25*(6), 1374–1379. https://doi.org/10.1093/beheco/aru131

Hoicka, E., Bijvoet-Van Den Berg, S., Kerr, T., & Carberry, M. (2013). The unusual box test: A non-verbal, non-representational divergent thinking test for toddlers. In *AAAI Spring Symposium - Technical Report* (Vol. SS-13-02, pp. 32–37). Retrieved from www.aaai.org

Holekamp, K. E., Swanson, E. M., & Meter, P. E. Van. (2013). Developmental constraints on behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(20120350), 1–11. https://doi.org/10.1098/rstb.2012.0350

Hommel, B. (2015). Between persistence and flexibility. In *Advances in Motivation Science* (pp. 33–67). Elsevier Inc. https://doi.org/10.1016/bs.adms.2015.04.003

Hopper, L. M., Kurtycz, L. M., Ross, S. R., & Bonnie, K. E. (2015). Captive chimpanzee foraging in a social setting: A test of problemsolving, flexibility, and spatial discounting. *PeerJ*, *2015*(3). https://doi.org/10.7717/peerj.833

Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal Cognition*, *17*(4), 835–847. https://doi.org/10.1007/s10071-013-0715-y

Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, *81*(6), 1195–1202. https://doi.org/10.1016/j.anbehav.2011.03.002

Hoppitt, W., & Laland, K. N. (2008). Social Processes Influencing Learning in Animals: A Review of the Evidence. In *Advances in the Study of Behavior* (Vol. 38, pp. 105–165). https://doi.org/10.1016/S0065-3454(08)00003-X

Hrdy, S. B. (1999). *Mother nature: A history of mothers, infants, and natural selection*. New York: Pantheon Books.

Hrdy, S. B. (2005). Comes the child before the man: Cooperative breeding and the evolution of prolonged post-weaning dependence. In B. Hewlett & M. Lamb (Eds.), *Hunter-gatherer*

*childhoods: Evolutionary, developmental, and cultural perspectives* (pp. 65–91). New Brunswick, NJ: Aldine/Transactions.

Hrdy, S. B. (2006). Evolutionary context of human development: the cooperative breeding model. In C. S. Carter, L. Ahnert, K. E. Grossmann, S. B. Hrdy, M. E. Lamb, S. W. Porges, & N. Sachser (Eds.), *Attachment and Bonding: A New Synthesis* (pp. 9–32). MIT Press. Retrieved from http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.207.8922&rep=rep1&type=pdf

Hrubesch, C., Preuschoft, S., & van Schaik, C. P. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (Pan troglodytes). *Animal Cognition*, *12*(2), 209–216. https://doi.org/10.1007/s10071-008-0183-y

Hubrecht, R. C. (1985). Home-range size and use and territorial behavior in the common marmoset, Callithrix jacchus jacchus, at the tapacura field station, recife, Brazil. *International Journal of Primatology*, *6*(5), 533–550. https://doi.org/10.1007/BF02735575

Huebner, F., & Fichtel, C. (2015). Innovation and behavioral flexibility in wild redfronted lemurs (Eulemur rufifrons). *Animal Cognition*, *18*(3), 777–787. https://doi.org/10.1007/s10071-015-0844-6

Huebner, F., Fichtel, C., & Kappeler, P. M. (2018). Linking cognition with fitness in a wild primate: fitness correlates of problem-solving performance and spatial learning ability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170295. https://doi.org/10.1098/rstb.2017.0295

Hurtubise, J. L., & Howland, J. G. (2017). Effects of stress on behavioral flexibility in rodents. *Neuroscience*, *345*, 176–192. https://doi.org/10.1016/j.neuroscience.2016.04.007

Izquierdo, A., Brigman, J. L., Radke, A. K., Rudebeck, P. H., & Holmes, A. (2017). The neural basis of reversal learning: An updated perspective. *Neuroscience*. https://doi.org/10.1016/j.neuroscience.2016.03.021

Jepma, M., Verdonschot, R. G., van Steenbergen, H., Rombouts, S. A. R. B., & Nieuwenhuis, S. (2012). Neural mechanisms underlying the induction and relief of perceptual curiosity. *Frontiers in Behavioral Neuroscience*, *6*(5), 1–9. https://doi.org/10.3389/fnbeh.2012.00005

Johnson-Ulrich, L., Johnson-Ulrich, Z., & Holekamp, K. (2018). Proactive behavior, but not

inhibitory control, predicts repeated innovation by spotted hyenas tested with a multi-access box. *Animal Cognition*, *21*(3), 379–392. https://doi.org/10.1007/s10071-018-1174-2

Johnson-Ulrich, Z. (2017). *Predictors of behavioral flexibility and problem-solving in carnivora*. Oakland University.

Jones, C. B. (2005). *Behavioral flexibility in primates. Causes and consequences*. (R. H. Tuttle, Ed.). New York: Springer. https://doi.org/10.1007/s10764-006-9035-2

Judge, P. G., & Essler, J. L. (2013). Capuchin monkeys exercise self-control by choosing token exchange over an immediate reward. *International Journal of Comparative Psychology*, *26*, 256–266.

Judge, P. G., Evans, D. W., Schroepfer, K. K., & Gross, A. C. (2011). Perseveration on a reversal-learning task correlates with rates of self-directed behavior in nonhuman primates. *Behavioural Brain Research*, *222*(1), 57–65. https://doi.org/10.1016/j.bbr.2011.03.016

Kabadayi, C., Bobrowicz, K., & Osvath, M. (2018). The detour paradigm in animal cognition. *Animal Cognition*. https://doi.org/10.1007/s10071-017-1152-0

Kahrs, B. A., & Lockman, J. J. (2014). Building tool use from object manipulation: A perception-action perspective. *Ecological Psychology*, *26*(1–2), 88–97. https://doi.org/10.1080/10407413.2014.874908

Kamilar, J. M., & Baden, A. L. (2014). What drives flexibility in primate social organization? *Behavioral Ecology and Sociobiology*, *68*(10), 1677–1692. https://doi.org/10.1007/s00265-014-1776-x

Kandel, A. W., Bolus, M., Bretzke, K., Bruch, A. A., Haidle, M. N., Hertler, C., & Märker, M. (2016). Increasing behavioral flexibility? An integrative macro-scale approach to understanding the Middle Stone Age of southern Africa. *Journal of Archaeological Method and Theory*, *23*(2), 623–668. https://doi.org/10.1007/s10816-015-9254-y

Kang, M. J., Hsu, M., Krajbich, I. M., Loewenstein, G., McClure, S. M., Wang, J. T. Y., & Camerer, C. F. (2009). The wick in the candle of learning: Epistemic curiosity activates reward circuitry and enhances memory. *Psychological Science*, *20*(8), 963–973. https://doi.org/10.1111/j.1467-9280.2009.02402.x

Kaufman, A., & Kaufman, J. (2014). Applying theoretical models on human creativity to animal

studies. *Animal Behavior and Cognition*, *1*(1), 77–89. https://doi.org/10.12966/abc.02.06.2014

Kemp, C., & Kaplan, G. (2013). Facial expressions in common marmosets (Callithrix jacchus) and their use by conspecifics. *Animal Cognition*, *16*(5), 773–788. https://doi.org/10.1007/s10071-013-0611-5

Kendal, R. L., Coe, R. L., & Laland, K. N. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology*, *66*(2), 167–188. https://doi.org/10.1002/ajp.20136

Kendal, Rachel L., Custance, D. M., Kendal, J. R., Vale, G., Stoinski, T. S., Rakotomalala, N. L., & Rasamimanana, H. (2010). Evidence for social learning in wild lemurs (Lemur catta). *Learning and Behavior*, *38*(3), 220–234. https://doi.org/10.3758/LB.38.3.220

Kern, J. M., & Radford, A. N. (2014). Sentinel dwarf mongooses, Helogale parvula, exhibit flexible decision making in relation to predation risk. *Animal Behaviour*, *98*, 185–192. https://doi.org/10.1016/j.anbehav.2014.10.012

Kidd, C., & Hayden, B. Y. (2015). The psychology and neuroscience of curiosity. *Neuron*, *88*(3), 449–460. https://doi.org/10.1016/j.neuron.2015.09.010

Knaebe, B., Taylor, A. H., Elliffe, D. M., & Gray, R. D. (2017). New Caledonian crows show behavioural flexibility when manufacturing their tools. *Behaviour*, *154*(1), 65–91. https://doi.org/10.1163/1568539X-00003411

Koebele, S. V., Mennenga, S. E., Hiroi, R., Quihuis, A. M., Hewitt, L. T., Poisson, M. L., … Bimonte-Nelson, H. A. (2017). Cognitive changes across the menopause transition: A longitudinal evaluation of the impact of age and ovarian status on spatial memory. *Hormones and Behavior*, *87*, 96–114. https://doi.org/10.1016/j.yhbeh.2016.10.010

Koski, S. E., & Burkart, J. M. (2015). Common marmosets show social plasticity and group-level similarity in personality. *Scientific Reports*, *5*. https://doi.org/10.1038/srep08878

Kozlovsky, D. Y., Branch, C. L., & Pravosudov, V. V. (2015). Problem-solving ability and response to novelty in mountain chickadees (Poecile gambeli) from different elevations. *Behavioral Ecology and Sociobiology*, *69*(4), 635–643. https://doi.org/10.1007/s00265-015-1874-4

Kuczaj II, S. A., & Horback, K. M. (2012). Play and emotion. In S. Watanabe & S. Kuczaj (Eds.),

*Emotions of Animals and Humans: Comparative Perspectives*. Japan: Springer.

Kudo, H., & Dunbar, R. I. M. (2001). Neocortex size and social network size in primates. *Animal Behaviour*, *62*(4), 711–722. https://doi.org/10.1006/anbe.2001.1808

Kunzler, J., Braun, K., & Bock, J. (2015). Early life stress and sex-specific sensitivity of the catecholaminergic systems in prefrontal and limbic regions of Octodon degus. *Brain Structure and Function*, *220*(2), 861–868. https://doi.org/10.1007/s00429-013-0688-2

Lameira, A. R., & Call, J. (2018). Time-space-displaced responses in the orangutan vocal system. *Science Advances*, *4*(11). https://doi.org/10.1126/sciadv.aau3401

Leal, M., & Powell, B. J. (2012). Behavioural flexibility and problem-solving in a tropical lizard. *Biology Letters*, *8*(1), 28–30. https://doi.org/10.1098/rsbl.2011.0480

Leavens, D. A., & Bard, K. (2019). Primate cognition in captivity. In A. Lock, C. Sinha, & N. Contier (Eds.), *Oxford Handbook of Human Symbolic Evolution*. Oxford University Press.

Lehner, S. R., Burkart, J. M., & van Schaik, C. P. (2011). Can captive orangutans (Pongo pygmaeus abelii) be coaxed into cumulative build-up of techniques? *Journal of Comparative Psychology*, *125*(4), 446–455. https://doi.org/10.1037/a0024413

Lermite, F., Peneaux, C., & Griffin, A. S. (2017). Personality and problem-solving in common mynas (Acridotheres tristis). *Behavioural Processes*, *134*, 87–94. https://doi.org/10.1016/j.beproc.2016.09.013

Leuner, B., & Gould, E. (2010). Dendritic growth in medial prefrontal cortex and cognitive flexibility are enhanced during the postpartum period. *Journal of Neuroscience*, *30*(40), 13499–13503. https://doi.org/10.1523/JNEUROSCI.3388-10.2010

Light, K. R., Grossman, H., Kolata, S., Wass, C., & Matzel, L. D. (2011). General learning ability regulates exploration through its influence on rate of habituation. *Behavioural Brain Research*, *223*(2), 297–309. https://doi.org/10.1016/j.bbr.2011.04.050

Lloyd, E. K. (2017). *Behavioral flexibility in the sanje mangabey (Cercocebus sanjei), Udzungwa Mountains, Tanzania*. The University of Texas at San Antonio.

Loewenstein, G. (1994). The psychology of curiosity: A review and reinterpretation. *Psychological Bulletin*, *116*(1), 75–98. https://doi.org/10.1037/0033-2909.116.1.75

Logan, C. J. (2016a). Behavioral flexibility and problem solving in an invasive bird. *PeerJ*, *4*,

e1975. https://doi.org/10.7717/peerj.1975

Logan, C. J. (2016b). How far will a behaviourally flexible invasive bird go to innovate? *Royal Society Open Science*, *3*(6). https://doi.org/10.1098/rsos.160247

Loukola, O. J., Perry, C. J., Coscos, L., & Chittka, L. (2017). Bumblebees show cognitive flexibility by improving on an observed complex behavior. *Science*, *355*(6327). https://doi.org/10.1126/science.aag2360

Lourenco, F., & Casey, B. J. (2013). Adjusting behavior to changing environmental demands with development. *Neuroscience and Biobehavioral Reviews*, *37*(9), 2233–2242. https://doi.org/10.1016/j.neubiorev.2013.03.003

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

Lucon-Xiccato, T., & Bisazza, A. (2014). Discrimination reversal learning reveals greater female behavioural flexibility in guppies. *Biology Letters*, *10*(6), 1–4. https://doi.org/10.1098/rsbl.2014.0206

Lukas, D., & Clutton-Brock, T. (2012). Cooperative breeding and monogamy in mammalian societies. *Proceedings of the Royal Society B: Biological Sciences, 279(1736),* 2151-2156. https://doi.org/10.1098/rspb.2011.2468

MacLean, E. L., Hare, B., Nun, C. L., Addessi, E., Amic, F., Anderson, R. C., … Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(20). https://doi.org/10.1073/pnas.1323533111

Madden, J. R., Langley, E. J. G., Whiteside, M. A., Beardsworth, C. E., & Van Horik, J. O. (2018). The quick are the dead: Pheasants that are slow to reverse a learned association survive for longer in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 1–9. https://doi.org/10.1098/rstb.2017.0297

Maille, A., & Schradin, C. (2017). Ecophysiology of cognition: How do environmentally induced changes in physiology affect cognitive performance? *Biological Reviews*, *92*(2), 1101–1112. https://doi.org/10.1111/brv.12270

Mangalam, M., & Singh, M. (2013). Flexibility in food extraction techniques in urban free-ranging bonnet macaques, Macaca radiata. *PLoS ONE*, *8*(12), 1–10.

https://doi.org/10.1371/journal.pone.0085497

Manrique, H. M., & Call, J. (2015). Age-dependent cognitive inflexibility in great apes. *Animal Behaviour*, *102*, 1–6. https://doi.org/10.1016/j.anbehav.2015.01.002

Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. *Animal Behaviour*, *85*(1), 195–202. https://doi.org/10.1016/j.anbehav.2012.10.026

Marsh, L. K. (2003). *Primates in fragments: Ecology and conservation*. New York: Kluwer Academic/Plenum Publishers.

Mason, G., Burn, C. C., Dallaire, J. A., Kroshko, J., McDonald Kinkaid, H., & Jeschke, J. M. (2013). Plastic animals in cages: Behavioural flexibility and responses to captivity. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2013.02.002

Massen, J. J. M., Antonides, A., Arnold, A. M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology*, *75*(9), 947–958. https://doi.org/10.1002/ajp.22159

Mathot, K. J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*. https://doi.org/10.1111/j.1600-0706.2012.20339.x

Matsuzawa, T. (2007). Comparative cognitive development. *Developmental Science*, *10*(1), 97–103. https://doi.org/10.1111/j.1467-7687.2007.00570.x

McCabe, G. M., & Fedigan, L. M. (2007). Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female Cebus capucinus at Santa Rosa, Costa Rica. *International Journal of Primatology*, *28*(4), 837–851. https://doi.org/10.1007/s10764-007-9159-z

McFarland, R., Barrett, L., Boner, R., Freeman, N. J., & Henzi, S. P. (2014). Behavioral flexibility of vervet monkeys in response to climatic and social variability. *American Journal of Physical Anthropology*, *154*(3), 357–364. https://doi.org/10.1002/ajpa.22518

McLennan, M. R., Spagnoletti, N., & Hockings, K. J. (2017). The implications of primate behavioral flexibility for sustainable human–primate coexistence in anthropogenic habitats. *International Journal of Primatology*, *38*(2), 105–121.

https://doi.org/10.1007/s10764-017-9962-0

Mekonnen, A., Fashing, P. J., Sargis, E. J., Venkataraman, V. V., Bekele, A., Hernandez-Aguilar, R. A., … Stenseth, N. C. (2018). Flexibility in positional behavior, strata use, and substrate utilization among Bale monkeys (Chlorocebus djamdjamensis) in response to habitat fragmentation and degradation. *American Journal of Primatology*, *80*(5). https://doi.org/10.1002/ajp.22760

Ménard, N. (2002). Ecological plasticity of barbary macaques (Macaco sylvanus). *Evolutionary Anthropology*. https://doi.org/10.1002/evan.10067

Mettke-Hofmann, C., Wink, M., Winkler, H., & Leisler, B. (2005). Exploration of environmental changes relates to lifestyle. *Behavioral Ecology*, *16*(1), 247–254. https://doi.org/10.1093/beheco/arh159

Mikhalevich, I., Powell, R., & Logan, C. (2017). Is behavioural flexibility evidence of cognitive complexity? How evolution can inform comparative cognition. *Interface Focus*, *7*(20160121), 1–16. https://doi.org/10.1098/rsfs.2016.0121

Miller, K. E., Bales, K. L., Ramos, J. H., & Dietz, J. M. (2006). Energy intake, energy expenditure, and reproductive costs of female wild golden lion tamarins (Leontopithecus rosalia). *American Journal of Primatology*, *68*(11), 1037–1053. https://doi.org/10.1002/ajp.20306

Monchi, O., Petrides, M., Petre, V., Worsley, K., & Dagher, A. (2001). Wisconsin card sorting revisited: Distinct neural circuits participating in different stages of the task identified by event-related functional magnetic resonance imaging. *The Journal of Neuroscience*, *21*(19), 773–7741. https://doi.org/10.1523/JNEUROSCI.21-19-07733.2001

Monestier, C., Morellet, N., Verheyden, H., Gaillard, J. M., Bideau, E., Denailhac, A., … Hewison, A. J. M. (2017). Neophobia is linked to behavioural and haematological indicators of stress in captive roe deer. *Animal Behaviour*, *126*, 135–143. https://doi.org/10.1016/j.anbehav.2017.01.019

Montgomery, S. H. (2014). The relationship between play, brain growth and behavioural flexibility in primates. *Animal Behaviour*, *90*, 281–286. https://doi.org/10.1016/j.anbehav.2014.02.004

Moretti, L., Hentrup, M., Kotrschal, K., & Range, F. (2015). The influence of relationships on

neophobia and exploration in wolves and dogs. *Animal Behaviour*, *107*, 159–173. https://doi.org/10.1016/j.anbehav.2015.06.008

Moro-Rios, R. F., Meyer, A. L. S., Silva-Pereira, J. E., & Ludwig, G. (2018). Examining individual risk-taking in leontopithecus caissara (Primates, callitrichidae): Group order when arriving at and departing from sleeping sites. *Mastozoologia Neotropical*. https://doi.org/10.31687/SAREMMN.18.25.2.0.02

Moscovice, L. R., & Snowdon, C. T. (2006). The role of social context and individual experience in novel task acquisition in cottontop tamarins, Saguinus oedipus. *Animal Behaviour*, *71*(4), 933–943. https://doi.org/10.1016/j.anbehav.2005.09.007

Murai, T., Nakako, T., Ikejiri, M., Ishiyama, T., Taiji, M., & Ikeda, K. (2013). Effects of lurasidone on executive function in common marmosets. *Behavioural Brain Research*, *246*, 125–131. https://doi.org/10.1016/j.bbr.2013.02.019

Nicolakakis, N., Sol, D., & Lefebvre, L. (2003). Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour*, *65*(3), 445–452. https://doi.org/10.1006/anbe.2003.2085

Nilsson, J. Å., Åkesson, M., & Nilsson, J. F. (2009). Heritability of resting metabolic rate in a wild population of blue tits. *Journal of Evolutionary Biology*, *22*(9), 1867–1874. https://doi.org/10.1111/j.1420-9101.2009.01798.x

Nilsson, S. R. O., Alsiö, J., Somerville, E. M., & Clifton, P. G. (2015). The rat's not for turning: Dissociating the psychological components of cognitive inflexibility. *Neuroscience and Biobehavioral Reviews*, *56*, 1–14. https://doi.org/10.1016/j.neubiorev.2015.06.015

Nissen, H. W. (1930). A study of exploratory behavior in the white rat by means of the obstruction method. *Pedagogical Seminary and Journal of Genetic Psychology*, *37*(3), 361–376. https://doi.org/10.1080/08856559.1930.9944162

O'Connor, T., & Wong, H. Y. (2015). Emergent properties. In *The Stanford Encyclopedia of Philosophy*. Retrieved from https://plato.stanford.edu/entries/properties-emergent/

Okano, H., Hikishima, K., Iriki, A., & Sasaki, E. (2012). The common marmoset as a novel animal model system for biomedical and neuroscience research applications. *Seminars in Fetal and Neonatal Medicine*. https://doi.org/10.1016/j.siny.2012.07.002

Okanoya, K., Tokimoto, N., Kumazawa, N., Hihara, S., & Iriki, A. (2008). Tool-use training in a species of rodent: The emergence of an optimal motor strategy and functional understanding. *PLoS ONE*, *3*(3). https://doi.org/10.1371/journal.pone.0001860

Ormerod, B. K., & Galea, L. A. M. (2003). Reproductive status influences the survival of new cells in the dentate gyrus of adult male meadow voles. *Neuroscience Letters*, *346*(1–2), 25–28. https://doi.org/10.1016/S0304-3940(03)00546-9

Otani, Y., Sawada, A., & Hanya, G. (2014). Short-term separation from groups by male Japanese macaques: Costs and benefits in feeding behavior and social interaction. *American Journal of Primatology*, *76*(4), 374–384. https://doi.org/10.1002/ajp.22241

Overington, S. E., Morand-Ferron, J., Boogert, N. J., & Lefebvre, L. (2009). Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour*, *78*(4), 1001–1010. https://doi.org/10.1016/j.anbehav.2009.06.033

Palagi, E. (2006). Social play in bonobos (Pan paniscus) and chimpanzees (Pan troglodytes): Implications for natural social systems and interindividual relationships. *American Journal of Physical Anthropology*, *129*(3), 418–426. https://doi.org/10.1002/ajpa.20289

Parker, S. T. (2015). Re-evaluating the extractive foraging hypothesis. *New Ideas in Psychology*, *37*, 1–12. https://doi.org/10.1016/j.newideapsych.2014.11.001

Peretti, A. V., & Carrera, P. (2005). Female control of mating sequences in the mountain scorpion Zabius fuscus: Males do not use coercion as a response to unreceptive females. *Animal Behaviour*, *69*(2), 453–462. https://doi.org/10.1016/j.anbehav.2004.04.019

Perry, S. E., Barrett, B. J., & Godoy, I. (2017). Older, sociable capuchins (Cebus capucinus) invent more social behaviors, but younger monkeys innovate more in other contexts. *Proceedings of the National Academy of Sciences*, *114*(30), 7806–7813. https://doi.org/10.1073/pnas.1620739114

Phillips, K. A., Watson, C. M., Bearman, A., Knippenberg, A. R., Adams, J., Ross, C., & Tardif, S. D. (2019). Age-related changes in myelin of axons of the corpus callosum and cognitive decline in common marmosets. *American Journal of Primatology*, *81*(2). https://doi.org/10.1002/ajp.22949

Picq, J. L. (2007). Aging affects executive functions and memory in mouse lemur primates.

*Experimental Gerontology*, *42*(3), 223–232. https://doi.org/10.1016/j.exger.2006.09.013

Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology and Evolution*, *18*(5), 228–233. https://doi.org/10.1016/S0169-5347(03)00036-3

Pisula, W., Turlejski, K., & Charles, E. P. (2013). Comparative psychology as unified psychology: The case of curiosity and other novelty-related behavior. *Review of General Psychology*, *17*(2), 224–229. https://doi.org/10.1037/a0032938

Platt, M. L., Brannon, E. M., Briese, T. L., & French, J. A. (1996). Differences in feeding ecology predict differences in performance between golden lion tamarins (Leontopithecus rosalia) and Wied's marmosets (Callithrix kuhli) on spatial and visual memory tasks. *Animal Learning and Behavior*, *24*(4), 384–393. https://doi.org/10.3758/BF03199010

Price, E. C., & Feistner, A. T. C. (1993). Food sharing in lion tamarins: Tests of three hypotheses. *American Journal of Primatology*, *31*(3), 211–221. https://doi.org/10.1002/ajp.1350310306

Price, E. E., & Stoinski, T. S. (2007). Group size: Determinants in the wild and implications for the captive housing of wild mammals in zoos. *Applied Animal Behaviour Science*, *103*(3–4), 255–264. https://doi.org/10.1016/j.applanim.2006.05.021

Pritchard, D. J., Hurly, T. A., Tello-Ramos, M. C., & Healy, S. D. (2016). Why study cognition in the wild (and how to test it)? *Journal of the Experimental Analysis of Behavior*. https://doi.org/10.1002/jeab.195

Pryce, C. R., Dettling, A., Spengler, M., Spaete, C., & Feldon, J. (2004). Evidence for altered monoamine activity and emotional and cognitive disturbance in marmoset monkeys exposed to early life stress. In *Annals of the New York Academy of Sciences* (Vol. 1032, pp. 245–249). https://doi.org/10.1196/annals.1314.030

Pryce, C. R., Rüedi-Bettschen, D., Dettling, A. C., Weston, A., Russig, H., Ferger, B., & Feldon, J. (2005). Long-term effects of early-life environmental manipulations in rodents and primates: Potential animal models in depression research. *Neuroscience and Biobehavioral Reviews*. https://doi.org/10.1016/j.neubiorev.2005.03.011

Rachwani, J., Soska, K. C., & Adolph, K. E. (2017). Behavioral flexibility in learning to sit.

*Developmental Psychobiology*. https://doi.org/10.1002/dev.21571

Ragozzino, M. E. (2007). The contribution of the medial prefrontal cortex, orbitofrontal cortex, and dorsomedial striatum to behavioral flexibility. In *Annals of the New York Academy of Sciences* (Vol. 1121, pp. 355–375). https://doi.org/10.1196/annals.1401.013

Raine, N. E., & Chittka, L. (2012). No trade-off between learning speed and associative flexibility in bumblebees: A reversal learning test with multiple colonies. *PLoS ONE*, *7*(9). https://doi.org/10.1371/journal.pone.0045096

Ramsey, G., Bastian, M. L., & van Schaik, C. P. (2007). Animal innovation defined and operationalized. *Behavioral and Brain Sciences*, *30*(4), 393–407. https://doi.org/10.1017/S0140525X07002373

Rapaport, L. G. (1999). Provisioning of young in golden lion tamarins (Callitrichidae, Leontopithecus rosalia): A test of the information hypothesis. *Ethology*, *105*(7), 619–636. https://doi.org/10.1046/j.1439-0310.1999.00449.x

Ratcliffe, J. M., Fenton, M. B., & Shettleworth, S. J. (2006). Behavioral flexibility positively correlated with relative brain volume in predatory bats. *Brain, Behavior and Evolution*, *67*(3), 165–176. https://doi.org/10.1159/000090980

Rayburn-Reeves, R. M., Stagner, J. P., Kirk, C. R., & Zentall, T. R. (2013). Reversal learning in rats (Rattus norvegicus) and pigeons (Columba livia): Qualitative differences in behavioral flexibility. *Journal of Comparative Psychology*, *127*(2), 202–211. https://doi.org/10.1037/a0026311

Reader, S. M. (2015). Causes of individual differences in animal exploration and search. *Topics in Cognitive Science*, *7*(3), 451–468. https://doi.org/10.1111/tops.12148

Reader, S. M., & Laland, K. N. (2001). Primate innovation: Sex, age and social rank differences. *International Journal of Primatology*, *22*(5), 787–805. https://doi.org/10.1023/A:1012069500899

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(7), 4436–4441. https://doi.org/10.1073/pnas.062041299

Reader, S. M., & Laland, K. N. (Eds.). (2003). *Animal Innovation: an introduction*. New York:

Cambridge University Press.

Reader, S. M., & MacDonald, K. (2003). Environmental variability and primate behavioural flexibility. In S. M. Reader & K. N. Laland (Eds.), *Animal Innovation* (pp. 83–104). Oxford University Press. https://doi.org/10.1093/acprof

Reader, S. M., Morand-Ferron, J., & Flynn, E. (2016). Animal and human innovation: Novel problems and novel solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(20150182), 1–11. https://doi.org/10.1098/rstb.2015.0182

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Roberts, R. L., Jenkins, K. T., Lawler, T., Wegner, F. H., Norcross, J. L., Bernhards, D. E., & Newman, J. D. (2001). Prolactin levels are elevated after infant carrying in parentally inexperienced common marmosets. *Physiology and Behavior*, *72*(5), 713–720. https://doi.org/10.1016/S0031-9384(01)00430-9

Rodrigues, N. N., & Martinez, R. A. (2014). Wildlife in our backyard: interactions between Wied's marmoset Callithrix kuhlii (Primates: Callithrichidae) and residents of Ilhéus, Bahia, Brazil. *Wildlife Biology*, *20*(2), 91–96. https://doi.org/10.2981/wlb.13057

Rosati, A. G. (2017). Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in Cognitive Sciences*, *21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011

Rossmanith, E., Grimm, V., Blaum, N., & Jeltsch, F. (2006). Behavioural flexibility in the mating system buffers population extinction: Lessons from the lesser spotted woodpecker Picoides minor. *Journal of Animal Ecology*, *75*(2), 540–548. https://doi.org/10.1111/j.1365-2656.2006.01074.x

Roth, G., & Dicke, U. (2012). Evolution of the brain and intelligence in primates. In *Progress in Brain Research* (Vol. 195, pp. 413–430). https://doi.org/10.1016/B978-0-444-53860-4.00020-9

Roth, T. C., LaDage, L. D., & Pravosudov, V. V. (2010). Learning capabilities enhanced in harsh environments: a common garden approach. *Proceedings of the Royal Society B: Biological*

*Sciences*, *277*(1697), 3187–3193. https://doi.org/10.1098/rspb.2010.0630

Rothe, H., Koenig, A., & Darms, K. (1993). Infant survival and number of helpers in captive groups of common marmosets (Callithrix jacchus). *American Journal of Primatology*, *30*(2), 131–137. https://doi.org/10.1002/ajp.1350300205

Russell, A. L., Buchmann, S. L., & Papaj, D. R. (2017). How a generalist bee achieves high efficiency of pollen collection on diverse floral resources. *Behavioral Ecology*, *28*(4), 991–1003. https://doi.org/10.1093/beheco/arx058

Russon, A. E., Kuncoro, P., Ferisa, A., & Handayani, D. P. (2010). How Orangutans (Pongo pygmaeus) Innovate for Water. *Journal of Comparative Psychology*, *124*(1), 14–28. https://doi.org/10.1037/a0017929

Russon, A. E., Van Schaik, C. P., Kuncoro, P., Ferisa, A., Handayani, D. P., & Van Noordwijk, M. A. (2009). Innovation and intelligence in orangutans. In S. A. Wich, S. S. U. Atmoko, T. M. Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. https://doi.org/10.1093/acprof:oso/9780199213276.003.0020

Rylands, A. B. (Ed.). (1993). *Marmosets and tamarins: Systematics, behaviour, and ecology*. Oxford: Oxford University Press.

Rymer, T. L., Pillay, N., & Schradin, C. (2013). Extinction or survival? Behavioral flexibility in response to environmental change in the African striped mouse Rhabdomys. *Sustainability*, *5*, 163–186. https://doi.org/10.3390/su5010163

Sabbatini, G., Stammati, M., Tavares, M. C. H., & Visalberghi, E. (2008). Behavioral flexibility of a group of bearded capuchin monkeys (Cebus libidinosus) in the National Park of Brasília (Brazil): Consequences of cohabitation with visitors. *Brazilian Journal of Biology*, *68*(4), 685–693. https://doi.org/10.1590/S1519-69842008000400002

Santillán-Doherty, A. M., Muñóz-Delgado, J., Arenas, R., Márquez, A., & Cortés, J. (2006). Reliability of a method to measure novelty-seeking in nonhuman primates. *American Journal of Primatology*, *68*(11), 1098–1113. https://doi.org/10.1002/ajp.20310

Schradin, C., Vuarin, P., & Rimbach, R. (2018). The neoteny-helper hypothesis: When to expect and when not to expect endocrine mechanisms to regulate allo-parental care? *Physiology and Behavior*, *193*(December), 127–134. https://doi.org/10.1016/j.physbeh.2017.12.008

Schubiger, M. N., Kissling, A., & Burkart, J. M. (2016). How task format affects cognitive performance: a memory test with two species of New World monkeys. *Animal Behaviour*, *121*, 33–39. https://doi.org/10.1016/j.anbehav.2016.08.005

Schubiger, M. N., Wüstholz, F. L., Wunder, A., & Burkart, J. M. (2015). High emotional reactivity toward an experimenter affects participation, but not performance, in cognitive tests with common marmosets (Callithrix jacchus). *Animal Cognition*, *18*(3), 701–712. https://doi.org/10.1007/s10071-015-0837-5

Sherwood, C. C., Subiaul, F., & Zawidzki, T. W. (2008). A natural history of the human mind: Tracing evolutionary changes in brain and cognition. In *Journal of Anatomy* (Vol. 212, pp. 426–454). https://doi.org/10.1111/j.1469-7580.2008.00868.x

Shnitko, T. A., Allen, D. C., Gonzales, S. W., Walter, N. A. R., & Grant, K. A. (2017). Ranking cognitive flexibility in a group setting of rhesus monkeys with a set-shifting procedure. *Frontiers in Behavioral Neuroscience*, *11*. https://doi.org/10.3389/fnbeh.2017.00055

Siani, J. M. (2009). *Costs and benefits of cooperative infant care in wild golden lion tamarins (Leontopithecus rosalia)*. *ProQuest Dissertations and Theses*. https://doi.org/10.1017/CBO9781107415324.004

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, *19*(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Silva, P. A., & Melo, C. (2018). Foraging suggests high behavioral flexibility in the blue-winged parrotlet (Forpus xanthopterygius, Psittacidae) in response to fleshy fruit availability. *Ambiência - Revista Do Setor de Ciências Agrárias e Ambientais*, *14*(1), 186–202. https://doi.org/10.5935/ambiencia.2018.13.01

Simon, N. P. P., Diamond, A. W., & Schwab, F. E. (2003). Do northern forest bird communities show more ecological plasticity than southern forest bird communities in eastern Canada? *Ecoscience*, *10*(3), 289–296. https://doi.org/10.1080/11956860.2003.11682776

Simon, N. W., Gregory, T. A., Wood, J., & Moghaddam, B. (2013). Differences in response initiation and behavioral flexibility between adolescent and adult rats. *Behavioral Neuroscience*, *127*(1), 23–32. https://doi.org/10.1037/a0031328

Slack, C. (2014). *Social learning and the development of social foraging behavior in golden lion tamarins (Leontopithecus rosalia)*. Clemson University. Retrieved from https://tigerprints.clemson.edu/all_theses

Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, *85*(5), 1004–1011. https://doi.org/10.1016/j.anbehav.2012.12.031

Snowdon, C.T., & Roskos, T. R. (2017). Stick-weaving: Innovative behavior in tamarins (Saguinus oedipus). *Journal of Comparative Psychology*, *131*(2), 174–178. https://doi.org/10.1037/com0000071

Snowdon, Charles T. (2001). Social processes in communication and cognition in callitrichid monkeys: A review. *Animal Cognition*, *4*(3–4), 247–257. https://doi.org/10.1007/s100710100094

Sol, D., Bacher, S., Reader, S. M., & Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. In *American Naturalist* (Vol. 172). https://doi.org/10.1086/588304

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*(5), 1101–1112. https://doi.org/10.1016/j.anbehav.2013.01.023

Sol, D., & Lefebvre, L. (2000). Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, *90*(3), 599–605. https://doi.org/10.1034/j.1600-0706.2000.900317.x

Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour*, *63*(3), 495–502. https://doi.org/10.1006/anbe.2001.1953

Solomon, N. G., & French, J. A. (1997). *Cooperative breeding in mammals*. New York: Cambridge University Press.

Spaulding, B., & Hauser, M. (2005). What experience is required for acquiring tool competence? Experiments with two callitrichids. *Animal Behaviour*, *70*(3), 517–526.

https://doi.org/10.1016/j.anbehav.2004.11.024

Spinelli, S., Ballard, T., Gatti-McArthur, S., Richards, G. J., Kapps, M., Woltering, T., … Pryce, C. R. (2005). Effects of the mGluR2/3 agonist LY354740 on computerized tasks of attention and working memory in marmoset monkeys. *Psychopharmacology*, *179*(1), 292–302.

Starling, M. J., Branson, N., Thomson, P. C., & McGreevy, P. D. (2013). Age, sex and reproductive status affect boldness in dogs. *Veterinary Journal*, *197*(3), 868–872. https://doi.org/10.1016/j.tvjl.2013.05.019

Stevens, J. R., Hallinan, E. V., & Hauser, M. D. (2005). The ecology and evolution of patience in two New World monkeys. *Biology Letters*, *1*(2), 223–226. https://doi.org/10.1098/rsbl.2004.0285

Stoinski, T. S., & Beck, B. B. (2001). Spontaneous tool use in captive, free-ranging golden lion tamarins (Leontopitchecus rosalia rosalia). *Primates*, *42*(4), 319–326. https://doi.org/10.1007/BF02629623

Stök, J., Machacek, Z., & Ruther, J. (2015). Behavioural flexibility of the chemical defence in the parasitoid wasp Leptopilina heterotoma. *Science of Nature*, *102*. https://doi.org/10.1007/s00114-015-1317-0

Stone, S. (2018). The tuna herders. Retrieved from https://www.biographic.com/posts/sto/the-tuna-herders

Sweeney, J. A., Rosano, C., Berman, R. A., & Luna, B. (2001). Inhibitory control of attention declines more than working memory during normal aging. *Neurobiology of Aging*, *22*(1), 39–47. https://doi.org/10.1016/S0197-4580(00)00175-5

Tapp, P. D., Siwak, C. T., Estrada, J., Head, E., Muggenburg, B. A., Cotman, C. W., & Milgram, N. W. (2003). Size and reversal learning in the beagle dog as a measure of executive function and inhibitory control in aging. *Learning and Memory*, *10*(1), 64–73. https://doi.org/10.1101/lm.54403

Tardif, S. D., & Richter, C. B. (1981). Competition for a desired food in family groups of the common marmoset (Callithrix jacchus) and the cotton-top tamarin (Saguinus oedipus). *Laboratory Animal Science*, *31*(1), 52–55.

Taylor, H., & Vickers, P. (2017). Conceptual fragmentation and the rise of eliminativism.

*European Journal for Philosophy of Science*, *7*(1), 17–40. https://doi.org/10.1007/s13194-016-0136-2

Tebbich, S., Stankewitz, S., & Teschke, I. (2012). The relationship between foraging, learning abilities and neophobia in two species of Darwin's finches. *Ethology*, *118*(2), 135–146. https://doi.org/10.1111/j.1439-0310.2011.02001.x

Tebbich, S., Stereln, K., & Teschke, I. (2010). The tale of the finch: Adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1543), 1099–1109. https://doi.org/10.1098/rstb.2009.0291

Tebbich, S., & Teschke, I. (2014). Coping with uncertainty: Woodpecker finches (Cactospiza pallida) from an unpredictable habitat are more flexible than birds from a stable habitat. *PLoS ONE*, *9*(3). https://doi.org/10.1371/journal.pone.0091718

Tello-Ramos, M. C., Branch, C. L., Kozlovsky, D. Y., Pitera, A. M., & Pravosudov, V. V. (2019). Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. *Animal Behaviour*, *147*, 129–136. https://doi.org/10.1016/j.anbehav.2018.02.019

Thornton, A., Mcauliffe, K., Dall, S. R. X., Fernandez-Duque, E., Garber, P. A., & Young, A. J. (2016). Fundamental problems with the cooperative breeding hypothesis. A reply to Burkart & van Schaik. *Journal of Zoology*, *299*(2), 84–88. https://doi.org/10.1111/jzo.12351

Thornton, Alex, & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459–1468. https://doi.org/10.1016/j.anbehav.2012.03.018

Titulaer, M., van Oers, K., & Naguib, M. (2012). Personality affects learning performance in difficult tasks in a sex-dependent way. *Animal Behaviour*, *83*(3), 723–730. https://doi.org/10.1016/j.anbehav.2011.12.020

Toussaint, E. F. A., Hendrich, L., Escalona, H. E., Porch, N., & Balke, M. (2016). Evolutionary history of a secondary terrestrial Australian diving beetle (Coleoptera, Dytiscidae) reveals a lineage of high morphological and ecological plasticity. *Systematic Entomology*, *41*(3), 650–657. https://doi.org/10.1111/syen.12182

Trosvik, P., Rueness, E. K., De Muinck, E. J., Moges, A., & Mekonnen, A. (2018). Ecological plasticity in the gastrointestinal microbiomes of Ethiopian Chlorocebus monkeys. *Scientific*

*Reports*, *8*(1). https://doi.org/10.1038/s41598-017-18435-2

Tschudin, A. J.-P. C. (1998). *Relative neocortex size and its correlates in dolphins: comparisons with humans and implications for mental evolution.* University of Natal. Retrieved from http://researchspace.ukzn.ac.za/xmlui/handle/10413

Vale, Gill L., Flynn, E. G., Pender, L., Price, E., Whiten, A., Lambeth, S. P., … Kendal, R. L. (2016). Robust retention and transfer of tool construction techniques in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *130*(1), 24–35. https://doi.org/10.1037/a0040000

Vale, Gillian L., Flynn, E. G., Kendal, J., Rawlings, B., Hopper, L. M., Schapiro, S. J., … Kendal, R. L. (2017). Testing differential use of payoff-biased social learning strategies in children and chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1868). https://doi.org/10.1098/rspb.2017.1751

van Horik, J. O., & Madden, J. R. (2016). A problem with problem solving: Motivational traits, but not cognition, predict success on novel operant foraging tasks. *Animal Behaviour*, *114*, 189–198. https://doi.org/10.1016/j.anbehav.2016.02.006

van Leeuwen, E. J. C., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. M. (2013). Chimpanzees (Pan troglodytes) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PLoS ONE*, *8*(11). https://doi.org/10.1371/journal.pone.0080945

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., … Merrill, M. (2003). *Orangutan cultures and the evolution of material culture*. *Science* (Vol. 299).

van Schaik, C. P., Burkart, J. M., Damerius, L. A., Forss, S. I. F., Koops, K., van Noordwijk, M. A., & Schuppli, C. (2016). The reluctant innovator: orangutans and the phylogeny of creativity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150183. https://doi.org/10.1098/rstb.2015.0183

Veit, L., Pidpruzhnykova, G., & Nieder, A. (2015). Associative learning rapidly establishes neuronal representations of upcoming behavioral choices in crows. *Proceedings of the National Academy of Sciences*, *112*(49), 15208–15213. https://doi.org/10.1073/pnas.1509760112

Vickery, S. S., & Mason, G. J. (2003). Behavioral persistence in captive bears: implications for

reintroduction. *Ursus*, *14*(1), 35–43.

Vlamings, P. H. J. M., Hare, B., & Call, J. (2010). Reaching around barriers: The performance of the great apes and 3-5-year-old children. *Animal Cognition*, *13*(2), 273–285. https://doi.org/10.1007/s10071-009-0265-5

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, *60*(2), 195–202. https://doi.org/10.1006/anbe.2000.1457

Voelkl, B., & Huber, L. (2007). Common marmosets (Callithrix jacchus) do not utilize social information in three simultaneous social foraging tasks. *Animal Cognition*, *10*(2), 149–158. https://doi.org/10.1007/s10071-006-0053-4

Wallis, J. D., Dias, R., Robbins, T. W., & Roberts, A. C. (2001). Dissociable contributions of the orbitofrontal and lateral prefrontal cortex of the marmoset to performance on a detour reaching task. *European Journal of Neuroscience*, *13*(9), 1797–1808. https://doi.org/10.1046/j.0953-816x.2001.01546.x

Wang, M. Z., & Hayden, B. Y. (2019). Monkeys are curious about counterfactual outcomes. *Cognition*, *189*, 1–10. https://doi.org/10.1016/j.cognition.2019.03.009

Wang, M. Z., Marshall, A. T., & Kirkpatrick, K. (2017). Differential effects of social and novelty enrichment on individual differences in impulsivity and behavioral flexibility. *Behavioural Brain Research*, *327*, 54–64. https://doi.org/10.1016/j.bbr.2017.03.028

Weed, M. R., Bryant, R., & Perry, S. (2008). Cognitive development in macaques: Attentional set-shifting in juvenile and adult rhesus monkeys. *Neuroscience*, *157*(1), 22–28. https://doi.org/10.1016/j.neuroscience.2008.08.047

Werdenich, D., & Huber, L. (2002). Social factors determine cooperation in marmosets. *Animal Behaviour*, *64*, 771–781. https://doi.org/10.1006/anbe.2002.2001

Wergård, E. M., Westlund, K., Spångberg, M., Fredlund, H., & Forkman, B. (2016). Training success in group-housed long-tailed macaques (Macaca fascicularis) is better explained by personality than by social rank. *Applied Animal Behaviour Science*, *177*, 52–58. https://doi.org/10.1016/j.applanim.2016.01.017

West, R., & Alain, C. (2000). Age-related decline in inhibitory control contributes to the increased Stroop effect observed in older adults. *Psychophysiology*, *37*(2), 179–189.

https://doi.org/10.1017/S0048577200981460

Westbrook, S. R., Hankosky, E. R., Dwyer, M. R., & Gulley, J. M. (2018). Age and sex differences in behavioral flexibility, sensitivity to reward value, and risky decision-making. *Behavioral Neuroscience*, *132*(2), 75–87. https://doi.org/10.1037/bne0000235

Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, *11*(2), 233–244. https://doi.org/10.1017/S0140525X00049682

Whiten, Andrew, Custance, D. M., Gomez, J. C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *110*(1), 3–14. https://doi.org/10.1037/0735-7036.110.1.3

Wood, L. A., Kendal, R. L., & Flynn, E. G. (2015). Does a peer model's task proficiency influence children's solution choice and innovation? *Journal of Experimental Child Psychology*, *139*, 190–202. https://doi.org/10.1016/j.jecp.2015.06.003

Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L., & Russello, M. A. (2010). Behavioral flexibility and species invasions: The adaptive flexibility hypothesis. *Ethology Ecology and Evolution*, *22*(4), 393–404. https://doi.org/10.1080/03949370.2010.505580

Wu, X., Yang, W., Tong, D., Sun, J., Chen, Q., Wei, D., … Qiu, J. (2015). A meta-analysis of neuroimaging studies on divergent thinking using activation likelihood estimation. *Human Brain Mapping*, *36*(7), 2703–2718. https://doi.org/10.1002/hbm.22801

Yamamoto, M. E., & Box, H. (1997). The role of non-reproductive helpers in infant care in captive Callithrix jacchus. *Ethology*, *103*(9), 760–771. https://doi.org/10.1111/j.1439-0310.1997.tb00184.x

Yamamoto, M. E., & De Araújo Lopes, F. (2004). Effect of removal from the family group on feeding behavior by captive Callithrix jacchus. *International Journal of Primatology*, *25*(2), 489–500. https://doi.org/10.1023/B:IJOP.0000019164.98756.9c

Yamazaki, Y., Iriki, A., & Watanabe, S. (2011). Modulation of physical understanding by common marmosets (Callithrix jacchus). *Animal Cognition*, *14*(2), 175–186. https://doi.org/10.1007/s10071-010-0351-8

Yanagi, A., & Berman, C. M. (2017). Does behavioral flexibility contribute to successful play

among juvenile rhesus macaques? *Behavioral Ecology and Sociobiology*, *71*(10). https://doi.org/10.1007/s00265-017-2377-2

Zahed, S. R., Prudom, S. L., Snowdon, C. T., & Ziegler, T. E. (2008). Male parenting and response to infant stimuli in the common marmoset (Callithrix jacchus). *American Journal of Primatology*. https://doi.org/10.1002/ajp.20460

Zentall, T. R., Wasserman, E. A., & Urcuioli, P. J. (2014). Associative concept learning in animals. *Journal of the Experimental Analysis of Behavior*, *101*(1), 130–151. https://doi.org/10.1002/jeab.55

Zhang, Y., Cazakoff, B. N., Thai, C. A., & Howland, J. G. (2012). Prenatal exposure to a viral mimetic alters behavioural flexibility in male, but not female, rats. *Neuropharmacology*, *62*(3), 1299–1307. https://doi.org/10.1016/j.neuropharm.2011.02.022

Zinner, D., & Roos, C. (2014). So what is a species anyway? A primatological perspective. *Evolutionary Anthropology*, *23*(1), 21–23. https://doi.org/10.1002/evan.21390

Zuberogoitia, I., Martínez, J. E., Margalida, A., Gómez, I., Azkona, A., & Martínez, J. A. (2010). Reduced food availability induces behavioural changes in griffon vulture Gyps fulvus. *Ornis Fennica*, *87*(2), 52–60.

Zürcher, Y., & Burkart, J. M. (2017). Evidence for dialects in three captive populations of common marmosets (Callithrix jacchus). *International Journal of Primatology*, *38*(4), 780–793. https://doi.org/10.1007/s10764-017-9979-4